# Influence of Sky Conditions on Carbon Dioxide Uptake by Forests

Sigrid Dengel

Doctor of Philosophy
The University of Edinburgh
2009

Die Wissenschaft braucht Zusammenarbeit,
in der sich das Wissen des einen
durch die Entdeckung des anderen
bereichert.

José Ortega y Gasset (1883 - 1955)

## Declaration

I declare that this thesis has been composed by myself and has not been submitted in any previous application for a degree. The work described is my own except where stated otherwise.

Sigrid Dengel
September 2009

## Abstract

Sky conditions play an important role in the Earth's climate system, altering the solar radiation reaching the Earth's surface and determining the fraction of incoming direct and diffuse radiation. Sky conditions dictate the radiation distribution inside plant canopies and also the carbon dioxide uptake by forests during the growing season. On the long term these diffuse conditions may have a positive influence on forest growth in Northern Britain during the last 50 years.

We compared the quantity (amount) and quality (spectral distribution) of direct and diffuse radiation above, inside and below a forest stand under sunny, cloudy and overcast conditions in a thinned Sitka spruce [*Picea sitchensis (Bong.) Carr.*] forest (28 years, with an leaf area index (LAI) of around 5 $m^2m^{-2}$). Similar radiation properties (sky conditions) were used for analysis of light response and canopy conductance measurements in the same and also in a different spruce forest of the same species (33 years, LAI of around 7 $m^2 m^{-2}$) over the growing season 2008 in order to compare canopy activity under these conditions. In order to integrate short-term and long-term studies, we were looking at how far these conditions are influencing forest growth over several decades. To do so, we used freshly cut tree discs of Sitka spruce from a felled forest (planting year 1953) in southern Scotland and solar direct and diffuse radiation along with other meteorological data from the nearest meteorological station.

Our analysis show that the amount and quality of solar radiation is distributed differently inside forest stands under various sky conditions, leading to an enhanced carbon dioxide uptake and canopy stomatal activity under diffuse cloudy and overcast conditions. Furthermore we demonstrated which factors have influenced diffuse radiation distribution over the past 50 years and how these are correlated with forest growth in southern Scotland.

## Acknowledgements

I would like to thank most my parents Ute and Hansgeorg Dengel and my entire family for being there for me, always supporting me and my studies and for giving me the opportunity to follow my dreams. Prof John Grace, my supervisor I thank for giving me the opportunity to undertake this wonderful research at the University of Edinburgh and Prof John Moncrieff for giving me the chance to carry out research at a second forest research site, after a major setback. The same can be said to Dr Barry Gardiner and Dr Mike Perks for providing me with freshly cut Sitka spruce tree discs which became indispensable for my entire PhD project.
I thank Dr Terry Dawson for allowing me to use his TRAC device over two seasons in Griffin Forest.

Furthermore I would like to thank Dr Robert Clement for his help on countless occasions, be it with Matlab or in Harwood or Griffin Forest. A big thank you goes to Robert Howard and Graham Walker for their amazing support in the lab and in the field. I would like to also thank my wonderful partner Chris for always being there for me and for keeping me sane during all this time!

Last but not least I would like to thank the University of Edinburgh for awarding me a Torrance Research Scholarship and a College of Science and Engineering Studentship and School of GeoSciences Teaching Studentship. This work forms part of the research supported by the European Commission (CarboEurope-IP project).
Further financial support was provided by the National Environmental Research Council Centre for Terrestrial Carbon Dynamics (NERC CTCD).

## Table of Contents

## List of Figures

## List of Tables

## Glossary of Acronyms

| | |
|---|---|
| ℃ | Degree Celsius |
| $\beta$ | Bowen ratio |
| $\zeta$ | Photoequilibrium (R:FR) |
| $\omega$ | Vertical wind speed |
| $\rho_{\alpha}$ | Density of dry air |
| $\nu$ | Frequency |
| $\lambda$ | Wavelenght |
| $\lambda E$ | Spectral irradiance |
| $\kappa$ | Light attenuation coefficient |
| $\gamma$ | Psychrometric constant |
| $\mu$ | Micro |
| $\tau$ | Light transmissivity |
| $\tau_{B}$ | Transmissivity of blue light |
| $\tau_{Clear}$ | Transmissivity of blue light under clear sky conditions |
| $\tau_{Sky}$ | Transmissivity of blue light under various diffuse sky conditions |
| $A_{max}$ | Maximum gross photosynthesis at infinite irradiance |
| As | Altostratus |
| B | Blue light |
| BADC | British Atmospheric Data Centre |
| BGS | British Geological Survey |
| cLAI | Cumulative Leaf Area Index |
| $CO_2$ | Carbon dioxide |
| $c_p$ | Specific heat of air |
| CTCD | Centre for Terrestrial Carbon Dynamics |
| d | Zero plane displacement |
| $D_a$ | Saturation deficit |
| DBH | Diameter at breast height |
| e | base of the natural logarithm |
| EC | Eddy Covariance |
| $E\lambda$ | Latent heat |
| *f*APAR | Fraction of Absorbed Photosynthetic Active Radiation |
| $F_c$ | Flux density of scalar c ('carbon fluxes') |

| | |
|---|---|
| $F_{CO2}$ | Photosynthetic light response |
| FR | Far Red |
| FSF | Field Spectroscopy Facility (Edinburgh) |
| $g_a$ | Aerodynamic conductance |
| $g_c$ | Canopy conductance |
| GCR | Galactic Cosmic Rays |
| GEP | Gross Ecosystem Productivity |
| GI | Growth Index |
| GLA | Gap Light Analyzer |
| h | Height of canopy |
| $h$ | Planck's constant |
| $H_2O$ | Water vapour |
| Hz | Hertz |
| IRGA | Infra Red Gas Analyser |
| k | von Karman number |
| LAI | Leaf Area Index |
| LUE | Light Use Efficiency |
| m | Metre |
| $N_2$ | Nitrogen |
| NCEO | National Centre for Earth Observation |
| NEP | Net Ecosystem Productivity |
| NERC | National Environmental Research Council |
| nm | Nanometre |
| PAR | Photosynthetic Active Radiation |
| $Q_d$ | Incident diffuse radiation |
| $Q_g$ | Incident global radiation |
| R | Red |
| $R^2$ | Explained variance |
| $R_e$ | Ecosystem Respiration |
| $R_h$ | Relative humidity |
| s | Second |
| $s$ | Rate of the increase of saturation vapour pressure with air temperature |
| Sc | Stratocumulus |
| $S_w$ | Surface Wetness |
| $T_a$ | Air Temperature |

| | |
|---|---|
| TRAC | Tracing Radiation and the Architecture of Canopies |
| u | Wind speed |
| u* | Wind velocity |
| UK | United Kingdom |
| UKMO | United Kingdom Met Office |
| UV | Ultra Violet |
| VPD | Water Vapour Pressure Deficit |
| W | Watt |
| z | Height of measurements (top of tower) |
| $z_0$ | Surface roughness |

# Chapter 1

## Introduction and General Methodology

# 1. Introduction and General Methodology

## 1.1. Introduction

As the climate changes and the carbon dioxide ($CO_2$) concentration rises it is important to understand how forests and other extensive vegetation types respond to these changes. At the same time, a change in vegetation cover can influence the local climate, through modifying cloud cover, precipitation patterns, albedo, heat transfer and other factors. Environmental or anthropogenic changes also lead to a change in regional $CO_2$ fluxes, as ecosystems may act as a carbon sink or a carbon source (Schimel, 1995; Byrne & Green, 2004; Meir *et al.,* 2006). Forests belong to the most extensive biomes on the planet and are a substantial part of the biosphere, which is one of four major pools, along with fossil carbon, the oceans and the atmosphere, comprising the global carbon cycle (Smith *et al.,* 1993; Schimel, 1995; Waring & Running, 1998; Byrne & Green, 2004; Grace, 2004). Forests make up approximately 77% of the carbon contained in terrestrial vegetation (Byrne & Green, 2004) providing a total sink of around 0.6 - 0.7 Pg of carbon per year in forests of the Northern Hemisphere alone (Goodale *et al.,* 2002). The present research work is part of the CarboEurope-IP programme, which aims to understand better the current and future carbon balance of Europe at a local as well as on a continental scale, with a focus on the major ecosystems, viz. forests, grasslands, croplands and wetlands.

Forests act as carbon sinks and sources on a daily basis. During the day forests are acting as sinks, by removing carbon dioxide from the atmosphere via photosynthesis, and they act as sources during the night, when photosynthesis does not occur but respiratory processes continue, contributing to atmospheric carbon dioxide concentration. These fluxes are measured with the eddy covariance method (Moncrieff *et al.,* 1997; Aubinet *et al.,* 2000; Baldocchi, 2003), a micrometeorological technique, which can be used to determine whether an ecosystem is a carbon sink or source over time scales of a year or more (Ruimy *et al.,* 1995; Grace, 2004).

The atmosphere contains turbulent motions of upward and downward moving air that transport trace gases such as $CO_2$. The eddy covariance technique samples these turbulent motions to determine the net difference of material moving across the canopy-atmosphere interface (Baldocchi, 2003). Photosynthesis is primarily driven by the flux of solar radiation, but in recent years it has become apparent that sky conditions can appreciably influence the rate, with diffuse conditions having an enhancing effect (Gu *et al.,* 1999; Roderick *et al.,* 2001; Cohan *et al.,* 2002; Gu *et al.,* 2002; Farquhar & Roderick, 2003; Gu *et al.,* 2003; Niyogi *et al.,* 2004; Letts *et al.,* 2005; Min, 2005; Urban *et al.,* 2007; Mercado *et al.,* 2009).

Solar radiation which consists of electromagnetic waves entering the earth's atmosphere is attenuated by air molecules, water vapour and aerosols (Iqbal, 1983). Incoming solar radiation which interacts with particles and is scattered, reaches the Earth's surface as diffuse radiation. Particles suspended in the atmosphere that are smaller than the wavelength of the incident light (molecules) cause Rayleigh scattering (Gates, 1980; Iqbal, 1983; Monteith & Unsworth, 2008). This type of scattering is responsible for the appearance to the human eye of blue skies. The scattering which occurs when the solar beam strikes larger particles, such as dust, pollen, ash, is termed Mie scattering (Szeicz, 1974; Iqbal, 1983; Monteith & Unsworth, 2008) resulting in hazy and cloudy skies. The solar radiation spectrum can be partitioned into several wavebands, including the ultra-violet, visible light and the near infra-red bands (Weischet, 1995; Fabian, 2002).

Sky conditions including clouds, play an important role in the entire climate system (Warren *et al.,* 1985). Clouds alter the incoming solar radiation reaching the earth's surface determining the fraction of incoming direct and diffuse radiation. This aspect of the climate system was neglected for a very long time. Clouds, haze, mist and fog affect vegetation and the local climate by changing shading properties, precipitation patterns and the radiation regimes (Charlock & Sellers, 1980; Lohmann & Feichter, 2005).

Diffuse radiation represents not only a change in light quantity (amount) but also in light quality (spectral distribution) available for photosynthesis. Particles which have reflective or absorbing properties are altering the spectral distribution of irradiance recorded at the Earth's surface.

This incoming radiation is altered once more when it enters the forest canopy. Here, the foliage is again reflecting, absorbing and transmitting light, leading to yet another radiation field within the forest canopy and along the forest floor. Pioneers like Monsi and Saeki (1953) were among the first to investigate light penetration through a plant canopy, setting the foundation for numerous transmission studies (i.e. Perry *et al.,* 1969; Grace & Woolhouse, 1973; Norman & Jarvis, 1974; Lewandowska *et al.,* 1977; Sinclair & Knoerr, 1982; Kurachi *et al.,* 1993; Hale, 2001; Hale, 2003; Sonohat *et al.,* 2004). Radiation transmission and spectral distribution of radiation in plant canopies is affected by many factors, such as canopy structure and spectral properties of canopy elements (Federer & Tanner, 1966; Cowan, 1968; Muller, 1971; Norman & Jarvis, 1974; Norman & Jarvis, 1975; Smith and authors herein, 1982; Endler, 1993; Kurachi et al., 1993; Grant, 1997; Ni *et al.,* 1997; Hardy *et al.,* 2004; Sonohat *et al.,* 2004). These largely determine gas exchange and photosynthetic production (Sellers, 1985; Kurachi *et al.,* 1993).

In this work we investigated the above-canopy radiation regime, its penetration/transmittance through the canopy and absorption by the canopy under various weather scenarios. The key question is how these diverse sky conditions affect the radiation/light quality available to forests and how this can be related to the carbon dioxide uptake by plantations of Sitka spruce [*Picea sitchensis (Bong). Carr.*]. The species is a native of the west coast of North America (Waring & Franklin, 1979; Taylor, 1990; Pellatt & Mathewes, 1997) well adapted to the cool cloudy conditions of northern Britain.

Previous studies have mostly concentrated on diurnal and seasonal $CO_2$ exchange. In the present work we also consider growth. The visible evidence of carbon sequestration or accumulation in forests is forest growth itself.

Growth conditions change over years and decades, and the annual and periodic growth of needles, shoots and tree rings varies considerably (Spiecker, 1999). Active cell division in the vascular cambium layer produces cells which expand and displace the cambium in an outward direction. In trees from boreal and temperate latitudes, cambial activity is not constant throughout the year. This discontinuity causes the phenomenon of growth rings (Fritts, 1976; Creber, 1977; Schweingruber, 1988; Fritts, 1991). Yearly tree rings are added to the stem, recording the effect of the respective year's climatic conditions in which they grew. The standardised methodology in tree ring research is designed for the reconstruction of summer temperatures (Schove, 1954; Spiecker 1995; Briffa *et al.,* 1998; Kalela-Brundin, 1999; Gervais & MacDonald, 2001; Briffa *et al.,* 2002) or precipitation (Spiecker, 1995) over the past centuries. Tree rings have also been used as a proxy for galactic cosmic rays (Kirkby, 2007), about which we will say more later on.

By measuring carbon fluxes and carbon uptake by a forest stand during the growing season we are monitoring its seasonal biomass (carbon) accumulation. By incorporating tree ring research into the current study we are able to refer to an archive of yearly wood/carbon increment. This integration of short term and long-term studies serves the investigation of the possible link of climatological variables, such as diffuse radiation and forest growth, over several decades.

## 1.2. Aims & objectives

The aim of the PhD project is to develop relationships between carbon assimilation (photosynthesis) and sky conditions. Sky conditions vary with synoptic weather patterns and they include clear sunny periods/days, which are seen as periods where direct radiation is dominating the global radiation regime above the forest. Times where diffuse radiation is dominating incoming global radiation are cloudy or overcast conditions.

It is well known that diffuse light enhances canopy photosynthesis (Gu *et al.,* 1999; Roderick *et al.,* 2001; Gu *et al.,* 2002; Gu *et al.,* 2003; Farquhar & Roderick, 2003; Letts *et al.,* 2005, Urban *et al.,* 2007; Mercado *et al.,* 2009), but how far are these diverse conditions really influencing photosynthesis and the long term growth of coniferous forests? How does radiation distribution (amount and quality) change above a forest stand under these conditions and how is it distributed within the forest canopy? To what extent do interannual variations in sky conditions impact upon photosynthesis? This project will investigate these important attributes of sky conditions, in order to determine which aspect is stimulating carbon uptake. In which way do these distinctive conditions influence stomatal activity?

The linked hypotheses in this study are:

(i) Photosynthesis of Sitka spruce [*Picea sitchensis (Bong.) Carr.*] canopy is enhanced by diffuse radiation;

(ii) Stomatal conductance is enhanced by diffuse radiation;

(iii) Together, these effects of diffuse radiation may be seen in the analysis of growth rings, by reference to long term data on the direct and diffuse radiation over the British Isles.

## 1.3. Sites

In order to undertake the $CO_2$ flux and growth measurements envisaged in this project, several sites across Northern England, Southern and Central Scotland were chosen. They include a Sitka spruce [*Picea sitchensis (Bong.) Carr.*] plantation aged 15 – 36 years (Harwood Forest), a 28 year old Sitka spruce plantation located on a 7° slope in Central Scotland (Griffin Forest), a 53 year old Sitka spruce forest (Forest of Ae) which was felled in 2006. The Forest of Ae is located in the southern-western part of Scotland, 25 km west of Eskdalemuir (Fig. 1.1). To support the work on growth rings, the nearest Meteorological station for which long-term data on direct and diffuse solar radiation were available was Eskdalemuir, a Meteorological station run by the British Met Office (UKMO).

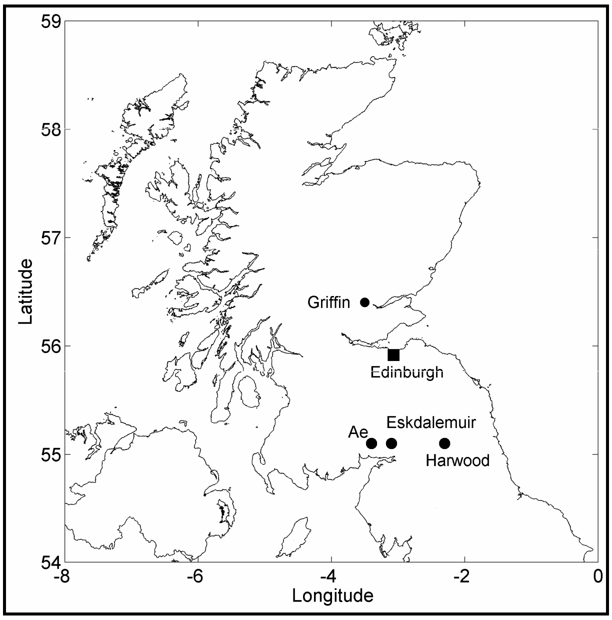


Figure 1.1: Location of research sites used in the current project.

### 1.3.1. Harwood Forest, Northumberland, England

Harwood Forest (Kielder Forest) in Northumberland, England (55°10′ N, 2°3′ W; 200 - 400 m asl.), is managed by the British Forestry Commission and Forest Enterprise. The research area is a Sitka spruce [*Picea sitchensis (Bong.) Carr*.] plantation, with stands aged between 15 and 36 years (Fig. 1.2). The research site is located in the 33 year old plot (planting year 1976), which has been partly row thinned 12 years ago. These canopy gaps are nearly closed although some areas are affected by wind throw.

A 28 m high scaffolding tower was erected to allow micrometeorological measurements above the canopy. A shed at the base of the tower houses the data logging system. This tower replaced a slender mast which was formerly used in a nearby location.

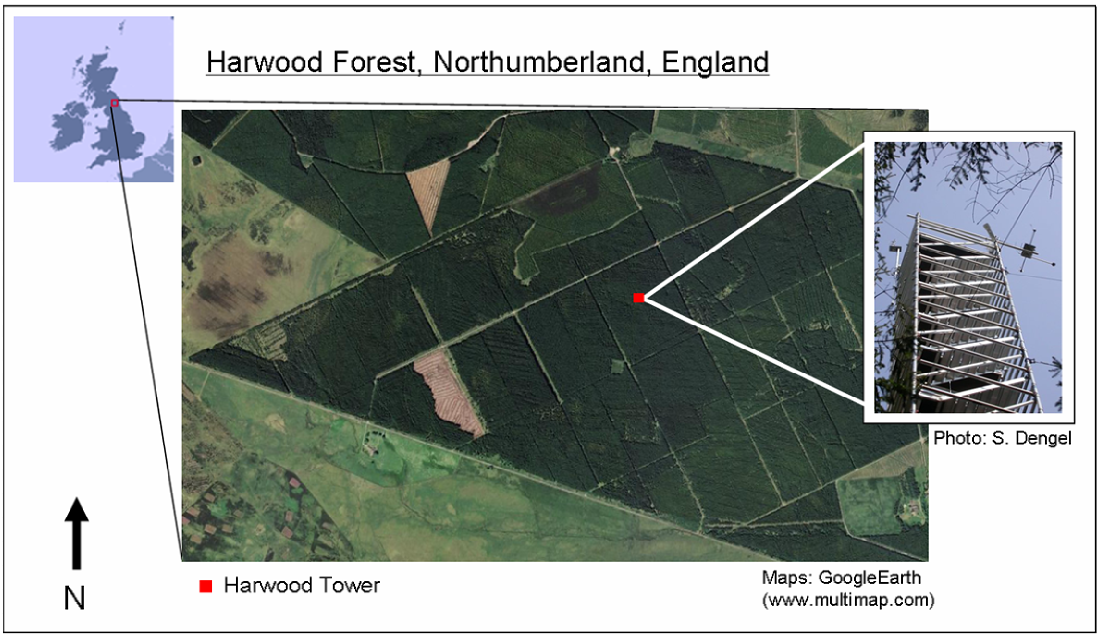


Figure 1.2: Harwood Forest research site.

The spruce trees were planted on a peaty gley soil (Zerva *et al.,* 2005) according to a mounding system (Ball *et al.,* 2007) with an approximate planting distance of 1.5 m. The current leaf area index (LAI) is around 7, a yield class of 16, with an average tree height of 22 m and an average diameter at breast height (DBH) of around 36 cm. Within the stand trees show a very high proportion of dead parts at the base of the canopy.

The original Harwood forest site was one of five UK sites in the CarboEurope-IP network. The entire network has over 100 representative European ecosystems measuring fluxes by a standardised protocol (Aubinet *et al.,* 2000). The CarboEurope-IP data sets are also represented in the world data base of FLUXNET**.** The site additionally is also a member of SPECNET, a network attempting to relate spectral reflectance to photosynthetic performance. Nationally the forest is also in use by the NERC Centre of Terrestrial Carbon Dynamics (CTCD). The new site has also been already integrated into Carboeurope-IP programme and its properties and data updated.

Micrometeorological measurements above the canopy include the operation of a fully equipped meteorological station as well as an eddy covariance system. The principle of eddy flux or eddy covariance is described in more detail in one of the subsequent chapters. The eddy covariance (EC) setup in Harwood includes a closed path system, described in Moncrieff *et al.* (1997), which contains the infra red gas analyser (IRGA) model Li-6262 (LI-COR, Lincoln, NE, USA) to measure carbon dioxide ($CO_2$), water vapour ($H_2O$) and latent heat fluxes ($\lambda E$). This setup uses Nitrogen ($N_2$) as a $CO_2/H_2O$ free reference gas. The ultrasonic anemometer used in this setup is manufactured by Gill (Solent R3, Gill Instruments, Lymington, UK). The eddy covariance data are acquired and saved onto a Laptop PC.

All meteorological data are recorded onto 2 CR10X and one CR3000 dataloggers (Campbell Scientific, Utah, USA). The meteorological station on top of the tower includes next to the standard meteorological sensors (temperature, humidity, precipitation (all Campbell Scientific, Utah, USA): net-radiation (NRLite, Kipp &

Zonen, Delft, NL), wind (Vector Instruments/ Skye Instruments, Llandrindod, UK) also a Delta-T BF3 sunshine sensor (direct and diffuse photosynthetic active radiation, PAR) (Delta-T Devices Ltd, Burwell, UK). Furthermore a Skye surface wetness sensor (occurrence of fog and dew) and 2 PAR sensors (down-welling and up-welling) (Skye Instruments, Llandrindod, UK) are installed.

A CNR1 pyranometer (Kipp & Zonen, Delft, NL) supplements the radiation measurements by giving separately short and long wave radiation measurements and the up-welling short and long wave radiation reflected or emitted by the ecosystem. Soil measurements include soil heat fluxes, temperature and moisture.

### 1.3.2. Griffin Forest, Perthshire, Scotland

A further forest used in this project is Griffin Forest (56°37′ N, 3° 48′ W; 380 m asl.). Like Harwood Forest, Griffin is also a major site within the Carboeurope-IP programme investigating the carbon fluxes of forests determining whether or not they are sinks or sources of carbon dioxide. This forest is part of Tay Forest Park, located in the Tay side area of Perthshire. It is a managed Sitka spruce forest planted between 1979 and 1983. The flux tower is located in the 28 year (in 2009) old stand on a 7° slope (Fig. 1.3). Further detailed description of the site can be found in Clement *et al.* (2003) and Clement (2004). The slope has been row-thinned in 2004 by removing every fifth tree resulting in straight thinning lines. In addition to the row thinning, selective thinning took place, removing in total around 30% of the biomass. Planting distance between trees is approx 2 m, resulting in an approximately 11 m distance from mid thinning line to the next. The Griffin Forest site has been in use by the University of Edinburgh since 1997 and it accommodates a well-managed eddy covariance system, as well as a fully equipped meteorological station. Both systems are located on top of a scaffolding walk-up tower running off solar panels, providing enough power to run the site all year round.

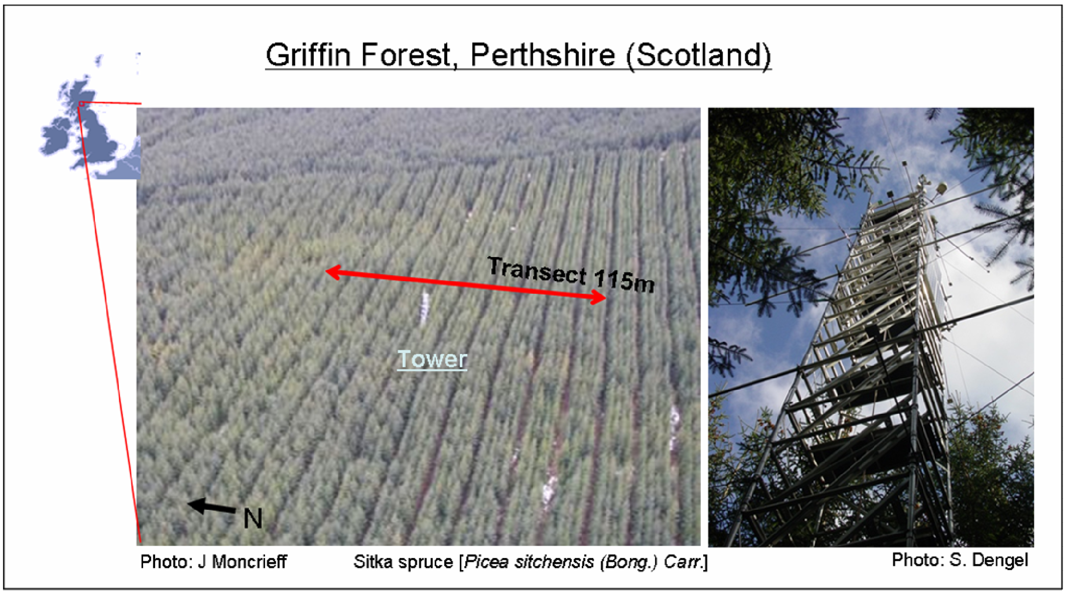


Figure 1.3: Griffin Forest, Scotland.

All meteorological data are recorded onto 3 Campbell dataloggers (Campbell CR10X, Campbell Scientific, Utah, USA). The meteorological station on top of the walk-up tower includes the same meteorological sensors as already described for Harwood forest. At the Griffin forest site a dome Solarimeter (CM5 Pyranometer - Kipp & Zonen, Delft, NL) is used for short and longwave incoming solar radiation.

In addition to the measurements recorded at the top of the canopy, Griffin accommodates a stationary transect consisting of 16 PAR (Photosynthetic Active Radiation) (Skye Instruments, Llandrindod, UK; LI-COR, Lincoln, NE, USA) sensors for below-canopy radiation measurements.

### 1.3.3. Forest of Ae, Dumfrieshire, Scotland

The 3rd forest site used in this work is the Forest of Ae (Fig. 1.4) in Dumfrieshire, Scotland, (55°12′ N; 3°35′ W; 350 m asl.). Forest of Ae is also a Sitka spruce [*Picea sitchensis (Bong.) Carr*.] forest and is commercially managed by the Forestry Commission. The plot, Queensberry - Auchenbue Burn, which is subject of the current study had been planted in 1953 and felled in February 2006.

The plot is a west facing slope, reaching over several altitudinal meters located in the central part of Forest of Ae.

Tree discs were collected in the Forest of Ae from 30 trees by the Forestry Commission's research agency Forest Research. They were kindly made available. These discs consist of 53 year rings, with 2005 being the last growth ring. The discs were kept in their original "wet" condition in the cold store of the Forest Research Northern Research Station, Roslin (Scotland). The trees have been felled and labelled according to Forest Research protocols (Mochan & Gardiner, 2007).

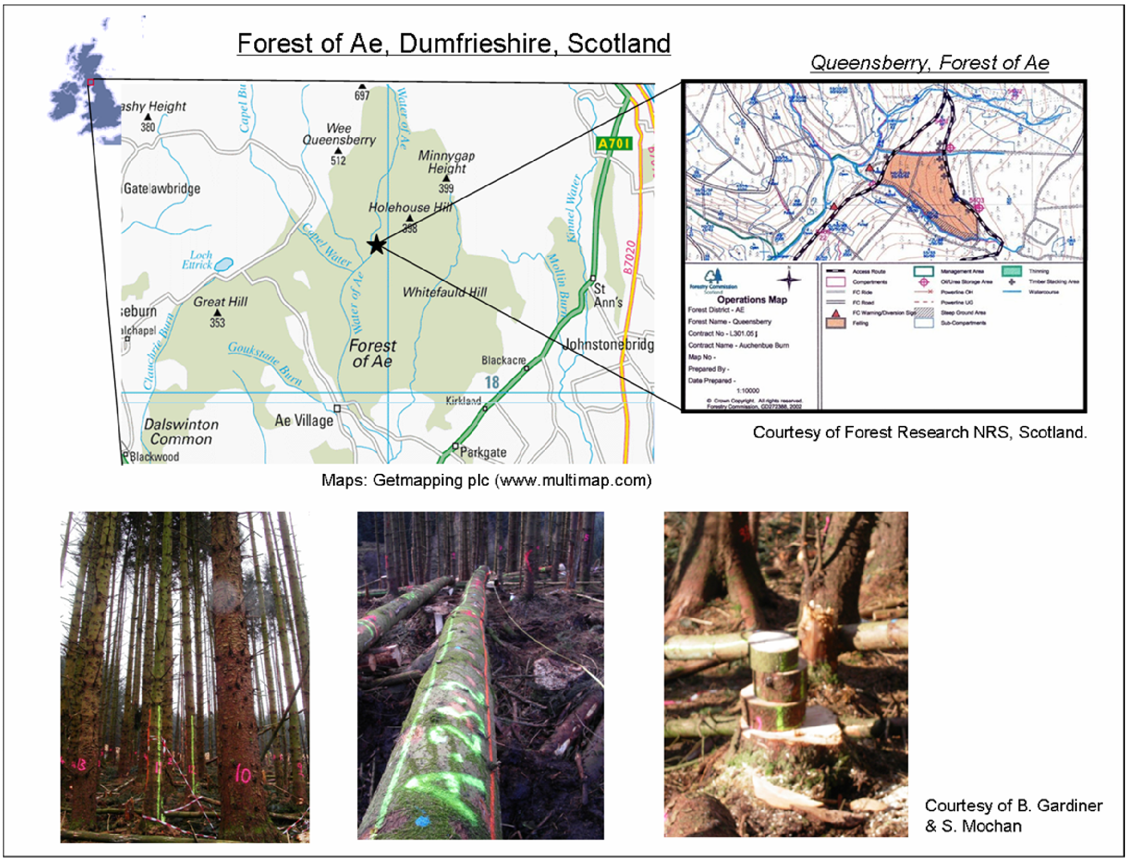


Figure 1.4: Forest of Ae location map: Queensberry plot.

### 1.3.4. Eskdalemuir Observatory, Dumfrieshire, Scotland

Eskdalemuir Observatory (Fig. 1.1 and Fig. 1.5) is operated by the British Geological Survey (BGS) and the British Met Office (UKMO). The observatory makes geomagnetic, seismological, meteorological and atmospheric electrical observations, mainly for monitoring changes in the natural magnetic field of the Earth, earthquake detection, and weather forecasting. It is the base for the Real Time Monitoring Centre for the Met Office network of automatic weather stations (Dawson, 2005; Aeby, 2007).

All meteorological data provided by the British Atmospheric Data Centre (BADC) have been quality controlled and originally handed over to the BADC by the British Met Office (UKMO).

Eskdalemuir is one of the oldest meteorological stations in the UK (Anonymous, 1909) and has the reputation of being the wettest and coldest station in Britain (Dawson, 2005). It has the longest diffuse radiation data set reaching back to the mid 1950's in the UK (Aeby, 2007). The observation station (55°16′ N; 3°10′ W; 245 m asl.) is located 25 km east of the Forest of Ae, the 3rd site integrated into the current project.

Fig. 1.5: Eskalemuir Observatory (Dawson, 2005).

## 1.4. Methods

### 1.4.1. Sky observations

A major aspect of the current project is the study of the ecosystem response to changes in sky conditions. In order to do this we recorded continuously, total (global) and diffuse photosynthetically active radiation (PAR) radiation at Harwood and Griffin forest. In the case of Forest of Ae we received diffuse radiation data (1956 – 2006) recorded at Eskdalemuir Observatory (Aeby, 2007).

Direct and diffuse radiation at Harwood and Griffin was recorded with a BF3 sunshine sensor (Delta-T Devices Ltd, Burwell, UK). This novel sensor, introduced only in 2001, uses an array of photodiodes and a computer-generated shader to separate the diffuse and the direct components of global radiation (Wood *et al.*, 2003; Muneer *et al.*, 2007).

Generally, diffuse radiation can be separated into dry diffuse and wet/humid diffuse. Fig. 1.6 gives a clear overview of these different types of radiation reaching the Earth's surface. Under dry (cloudy and hazy) conditions the majority of scattering happens higher in the atmosphere than the scattering of radiation under rainy and foggy conditions (wet). Under wet conditions scattering happens inside the canopy itself, producing a different light and radiation environment, compared to dry diffuse conditions.

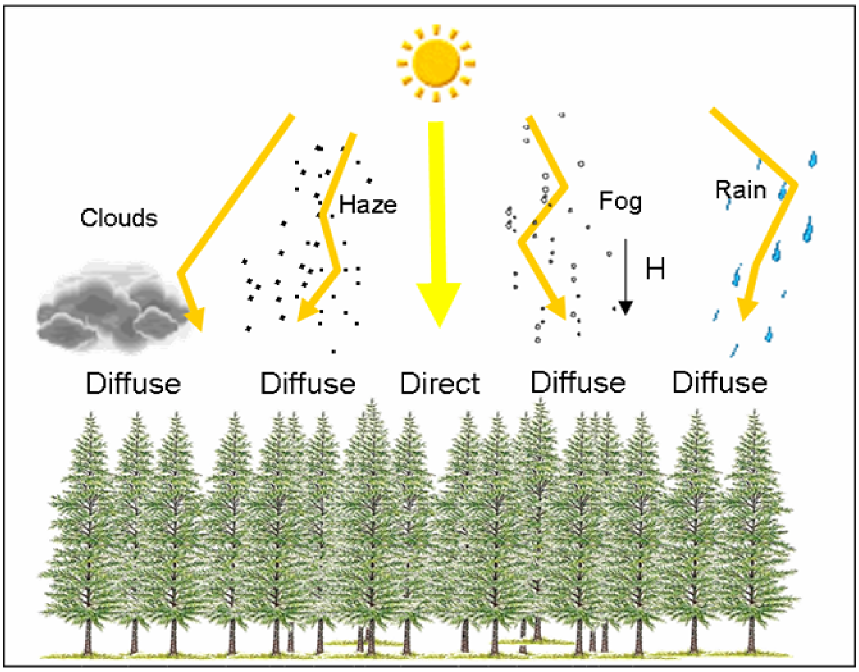


Figure 1.6: Direct and diffuse radiation reaching the ground. Direct radiation (solar beam) and diffuse (scattered) radiation of various types reaching the ground. The reproduction of the canopy is from Hecker (2006), reproduced with permission of the publisher BLV-Munich.

The light spectrum is partitioned into several wavebands, including ultra-violet, visible light and near infra-red bands (Weischet, 1995; Fabian, 2002). In order to receive information about the spectral distribution of the solar radiation recorded under various sky conditions at the top of the tower a field spectroradiometer (GER1500, Spectra Vista, New York, USA) equipped with a cosine diffuser was used. Due to its sensitivity to wet conditions this sensor was used only during particular measuring campaigns. Its exact setup and application will be described in a subsequent chapter.

During several measuring campaigns and experiments a Nikon digital camera (Coolpix4500, Nikon Corporation, Tokyo, Japan), with an attached fish eye lens (Fish-eye converter FC-E8, Nikon Corporation, Tokyo, Japan) was mounted to the top of the tower in Griffin (Fig. 1.7), providing visual information on sky conditions and their changes. These recorded images allow us to distinguish between cloud types and amount. Images taken before, during and/or after experiments are good indicators of cloud movements and high wind direction.

Image (a) (Fig. 1.7) shows a clear sky seen from the top of the tower, with the sonic anemometer and the dome solarimeter obstructing the vision. Image (b) shows a typical partly cloud covered sky and image (c) shows a completely cloud covered/overcast sky.

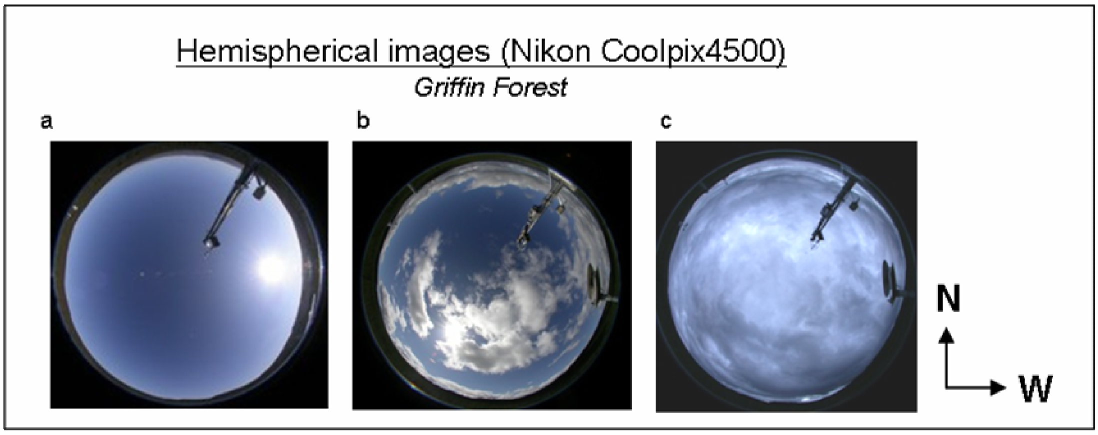


Figure 1.7: Hemispherical sky images taken under various sky conditions. (a) clear sky; (b) cloudy sky; (c) overcast sky. Photos: S. Dengel.

Cloud base/condensation level can be calculated from meteorological data and verified by comparison with the images taken at the respective time. Cloud types can also be inferred from high temporal resolution (10 min) radiation data following methods described in Haurwitz (1948); Falconer (1965); Duchon & O'Malley (1999); Calbo *et al.* (2001); Freedman *et al.* (2001) and Harrison *et al.* (2008).

### 1.4.2. Canopy structure

Another application of the digital camera and fish eye lens setup is the measurement of the leaf area index (LAI) and canopy structure. In order to record the most accurate values, images are taken according to protocols used by Chen *et al.* (1997); van Gardingen *et al.* (1999); Inoue *et al.* (2004); Jonckheere *et al.* (2004) and Gendron *et al.* (2006).

The ideal weather conditions for these images are overcast skies, in the early hours of the day or shortly after sunset. Images taken under sunny conditions are overexposed and can cause LAI calculations to underestimate the real leaf area value of the stand. However under sunny conditions light distribution within the stand becomes visible and phenomena like sunflecks recordable. These sunny gaps indicate areas on the forest floor where direct radiation is reaching the under-storey vegetation (Chazdon & Pearcy, 1991). These gaps can be divided into major sunflecks, where the sun is fully visible and penumbral sunflecks where the solar disc is only partially visible (Stenberg, 1995). The occurrence of these gaps with very high incident radiation values (Muller, 1971) are wind-dependent (Federer & Tanner, 1966; Chazdon & Pearcy, 1991) and they usually indicate areas with different spectral distributions (Morgan & Smith, 1978; Combes *et al.,* 2000) compared to shady areas.

Furthermore their appearance depends on the structure of the canopy itself (Norman & Jarvis, 1975; Mann & Curry, 1977; Morgan *et al.,* 1985; Chazdon & Pearcy, 1991). Pearcy (1990) indicates that sunflecks can be found more frequently where leaves are clumped at the end of branches. Clumped canopies are generally the rule in coniferous forests. Their wind dependency makes sunflecks very short lived in most cases, and plants on the forest floor therefore receive a rapidly fluctuating irradiance (Muller, 1971; Leakey *et al.,* 2003a, 2003b).

These changes have important implications on the photosynthesising canopy, since they have a different spectral distribution than shaded areas. These gaps are of physio-ecological importance to under-storey vegetation (Smith *et al.*, 1989; Leakey *et al.*, 2003b).

The Nikon Coolpix 4500 fitted with the FC-E8 converter-lens can "see" a solid angle of 180° (focal length equivalent to 7.2 mm), and such cameras are a standard way to record canopy structure (Fig. 1.8). To obtain such images the camera is mounted on a tripod 1 m above the ground and levelled with a common spirit level. Images are processed with Gap Light Analyzer (GLA) which is scientific image processing software (Forest Renewal BC, Frazer S., 1999). The top of images (a & c) are facing north, the right side indicates west.

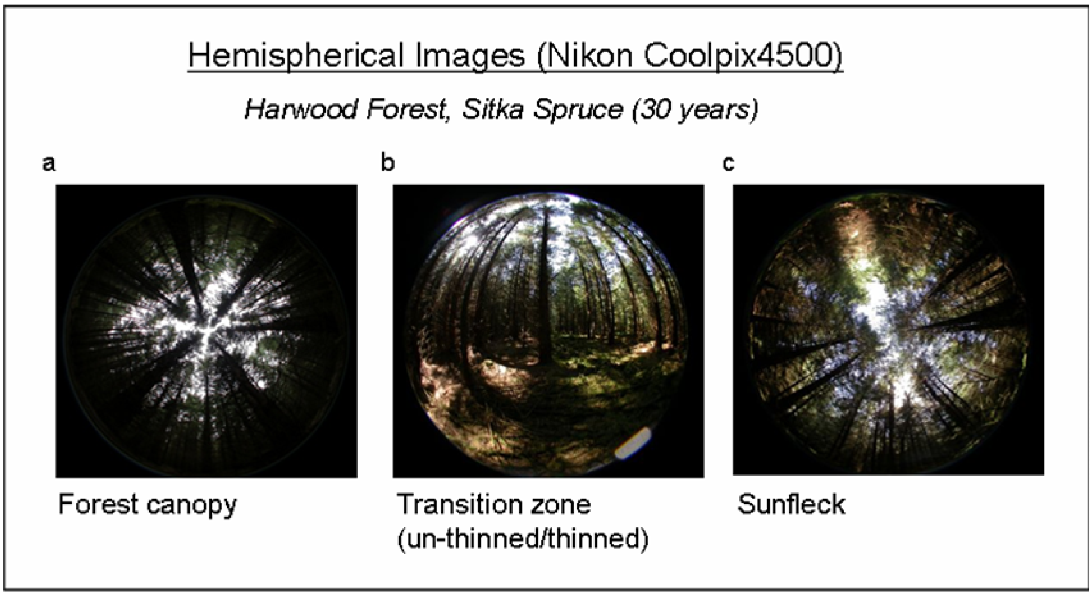


Figure 1.8: Hemispherical forest canopy images. Photos: S. Dengel. Image (a) shows a typical hemispherical image of a forest canopy, (b) an image of the transition zone between planted sections and thinned section (understorey vegetation) and (c) shows a hemispherical image of a Sitka spruce canopy with a visible sunfleck.

Fig. 1.8a shows a typical hemispherical image used for LAI calculations. For the calculations, the entire field of view is usually selected. Fig. 1.8b has been included in order to show the different ground cover below trees in areas where no thinning occurred and in areas where 1 row of trees had been removed. The 3rd image (Fig. 1.8c) would be of no use when calculating the leaf area, but images taken under sunny conditions are highly illustrative when working with light conditions inside forests under various sky conditions. In this case a large sunfleck has been recorded, i.e. a gap in which the solar beam could penetrate directly to the bottom of the forest canopy.

Norman & Jarvis (1974) describe the structure of a Sitka spruce forest canopy as a three level organization: (a) vertical distribution of leaf, branch and stem mass area; (b) angular distribution of needles on the shoots (inclination and orientation), and (c) the grouping of shoots into branches. However, in calculating LAI from hemispherical images or light attenuation, the basic theory assumes a random dispersion of leaves (Norman & Jarvis, 1975; Chen & Chilar, 1995; Gower *et al.*, 1999). We are working in a coniferous forest, where needles do not have a chaotic more-or-less random arrangement like broadleaved trees. So a correction value is used, known as the clumping index (van Gardingen *et al.,* 1999).

Another device used in order to record detailed canopy structure information is a TRAC (Tracing Radiation and the Architecture of Canopies) sensor (3rd Wave Engineering, Nepean, CND). TRAC is an optical instrument for measuring the leaf area index (LAI) and the fraction of photosynthetically active radiation (PAR) absorbed by the plant canopy (*ƒ*APAR). Exact theory description can be found in Chen & Cihlar (1995); Leblanc *et al.* (2002); Privette *et al.* (2002); Leblanc *et al. (*2005) and Leblanc (2008). This device is a hand-held sensor which is most effectively used on transect measurements. Furthermore it allows the measurement of canopy gap size distribution and canopy gap fraction. Gap fraction is the percentage of gaps in the canopy at a given solar zenith angle, the probability that a solar beam is reaching the ground without encountering any foliage (Li & Strahler, 1988; Smith *et al.*, 1989).

Gap size is the physical dimension of a gap in the canopy. Once the accumulated gap fraction is calculated, it is possible to remove the gaps in order to calculate LAI. This is then calculated or plotted as a random distributed canopy. The removed gap curve is brought to its closest agreement with the random canopy curve, and the resulting difference is the clumping index. The procedure described here is extracted and summarised from Chen & Cihlar (1995); Leblanc *et al.* (2002) and Leblanc (2008).

The clumping index value necessary for LAI calculations from hemispherical images increases with solar zenith angle (Chen & Chilar, 1995) and has been calculated from several transect measurements in Griffin forest during the growing season 2007 and 2008. These measurements apply mainly for hemispherical images taken over solar noon and we found for Sitka spruce, to be 0.98. This value, which is smaller than unity is resulting from more radiation having penetrated the spruce canopy than it would through a random canopy (Chen & Chilar, 1995).

A further method used in order to gather information on canopy structure, is the determination of the leaf area index along a vertical profile. The camera was mounted to a pole which was positioned away from the tower at various heights. Since the tower is obstructing each of these images, images were pre-processed prior to LAI analysis. All images have been halved to exclude the tower and then reconstructed after mirroring. This way we were able to estimate the vertical LAI distribution. All methods of LAI determination include stems. In deciduous trees the 'stem area index' is found during the leafless phase. In evergreen trees this is not possible. Norman & Jarvis (1974) estimated the ratio between stem & branches, as being the woody area to the total area including green and nongreen areas (Chen, 1996a, 1996b) for the same species to be 0.23. In the current study no correction for stem was made.

### 1.4.3. Field Spectroradiometry

Reliable measurements of radiation penetration through forest canopies involve the use of paired sensors (GER1500, Spectra Vista, New York, USA) fitted with cosine diffusers, permitting comparison of light availability in the understorey region with simultaneously measured light in an open area. This technique, however, requires a site where ambient light can be measured in the open, free from obstructions and edge effects (Capers & Chazdon, 2004).

The GER1500 instruments have a sampling resolution of 1.5 nm over the spectral range of 350 - 1050 nm. The spectral resolution is 3 nm which is recorded over 512 channels. The spectral resolution was effectively increased to 1 nm by applying post-processing methods, described in MacLellan (2006) and Walker (2009). This band width includes parts of the ultra-violet (300 - 380 nm), the visible light (380 - 750 nm) and parts of the far and near infra-red bands (750 - 1050 nm). A typical solar spectrum recorded on a clear day in Griffin forest (Scotland) is illustrated in Fig. 1.9. The standardised measurements using GER1500 field spectroradiometers include standard radiance and reflectance measurement procedures often used within remote sensing research (Nichol *et al.*, 2002; Szekielda *et al.*, 2003; Chen *et al.*, 2007). It requires a white reference panel. The target itself would usually be a leaf or a canopy.

The most common applied method is the single beam mode (Fogwill, 2005; MacArthur, 2006). However, there is a dual field of view technique requiring the bi-conical (standard lens) and the cos-conical (1 cosine diffuser, 1 standard lens) setup (MacArthur, 2007), whereby a paired set of spectroradiometers is required. Cos-conical measurements take additional sky values as the source of illumination in consideration as a reference. Here, the spectrometer pointing towards the sky is equipped with a cosine diffuser.

The target head is then used to take alternative measurements of a reference panel before scanning the target surface. A detailed description of field spectroscopy and its application history can be found in Milton *et al.* (2009).

None of these standard techniques could be used for our investigation. In order to fulfil the objectives of the current study, the measurement of incoming irradiance and its penetration through the forest canopy, a new method had to be applied. A novel approach is introduced here by introducing the cos-cos mode setup, wherein both spectrometers are equipped with cosine diffusers.

The difference between the new application and the standard paired setup described above is the equipping of both spectrometers with cosine diffusers pointing upwards, recording the spectral distribution of incoming solar radiation (irradiance) and radiation transmitted, reflected and scattered off forest foliage. Furthermore the traditional dual field of view setup where the paired sensors are controlled via one laptop was further modified in such a way that both spectrometers were used in a single view mode recording simultaneously (using a whistle as trigger signal). For our approach one device was pointing upwards recording sky light (stationary) (Fig. 1.9) while the second device (mobile) was also pointing upwards recording the same but also the radiance radiated by the abaxial (lower side of needles) side of forest foliage. The target measurement of the 'sky sensor' served as the reference value for the 'canopy sensor'. By using the target measurements of both sensors an exact transmissivity profile down the tower could be calculated. These measurements are similar to those of reflectance apart from the fact that our 'reflectance' measurements include features like absorption bands which are not visible in traditional standard reflectance spectra.

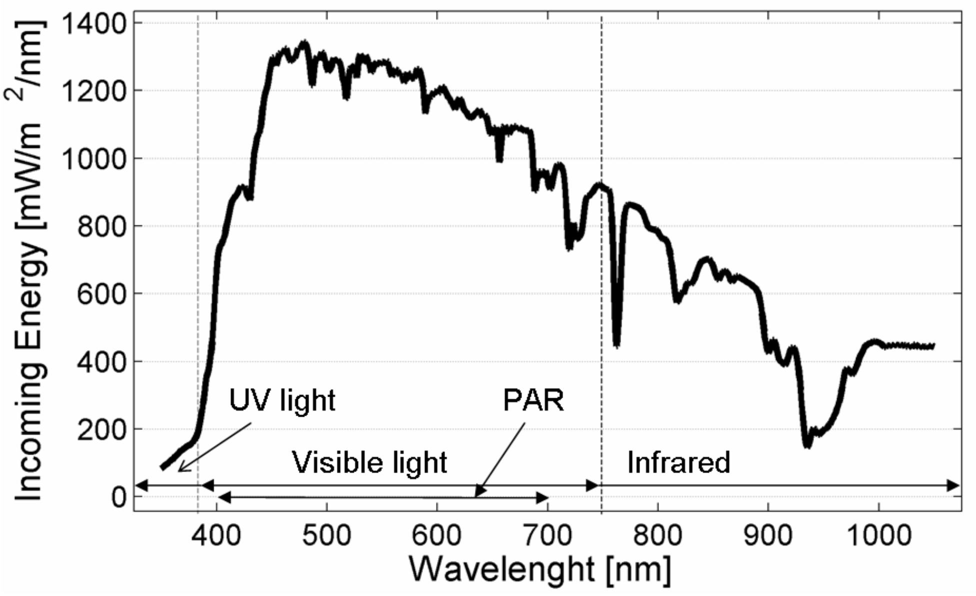


Figure 1.9: Solar spectrum recorded on a clear day in Griffin forest (Scotland), using the GER1500 sensor.

Several spectra were recorded at each metre down the tower, gathering information on above, within and below canopy spectral properties. As mentioned previously, Norman & Jarvis (1974) described the structure of a Sitka spruce forest canopy as a three level organisation. The vertical structure can be also divided into 3 levels: top-level, where the highest light exposure takes place including shoots and branches of a few years old only, the main canopy composed of alive and dead canopy and the lowest part of the forest canopy, mainly dead branches and stem. All three levels have different radiative properties. For coniferous forests the clumping of shoots into horizontal whorls of branches result in a non-random distribution of canopy elements within the crowns. The existence of a horizontal whorl structure allows more light to pass through the canopy without being scattered (Ni *et al.*, 1997).

Measurements were undertaken on various occasions under different sky conditions in order to investigate spectral distribution above, within and below the canopy.

### 1.4.4. Eddy Covariance

One of the main tasks in this study is the measurement of carbon dioxide ($CO_2$) and water vapour ($H_2O$) fluxes. In order to do this we are using the eddy covariance (EC) method, a micrometeorological technique (Aubinet *et al.,* 2000). The atmosphere contains turbulent motions of upward and downward moving air that transport trace gases such as $CO_2$. The eddy covariance technique samples these turbulent motions many times a second to determine the net difference of material moving vertically across the canopy-atmosphere interface (Baldocchi, 2003). A simple sketch can be seen in Fig. 1.10.

The eddy covariance method provides the measurements of the vertical flux of transported air parcels by correlation of the fluctuations in $CO_2$ concentration (in our case) with fluctuations in the vertical wind speed (Desjardins & Lemon, 1974). Detailed historical development of the technique can be found in Priestley & Swinbank (1947) with further improved and theoretical descriptions in Desjardins & Lemon (1974); Jarvis (1975); Bakan (1978); Baldocchi *et al.* (1988); Moncrieff *et al.* (1997); Aubinet *et al.* (2000) and Baldocchi (2003). A highly simplified way of writing the eddy flux of carbon dioxide and water vapour can be found in Moncrieff *et al.* (1997):

$$F_c = \overline{\omega\rho_c} + correction\ terms\,. \tag{1}$$

$F_c$ is representing the flux density of scalar *c*, in our case carbon dioxide. $\omega$ is the instantaneous vertical wind speed and $\rho_c$ is the corresponding density (or concentration) of the scalar *c.* The over-bar in eqn. (1) represents the mean of the product over the sampling interval (Moncrieff *et al.,* 1997). It has been found that statistically reliable data are recorded when averages are made over 30 minutes, although the solar irradiance under cloudy skies can fluctuate over much smaller intervals.

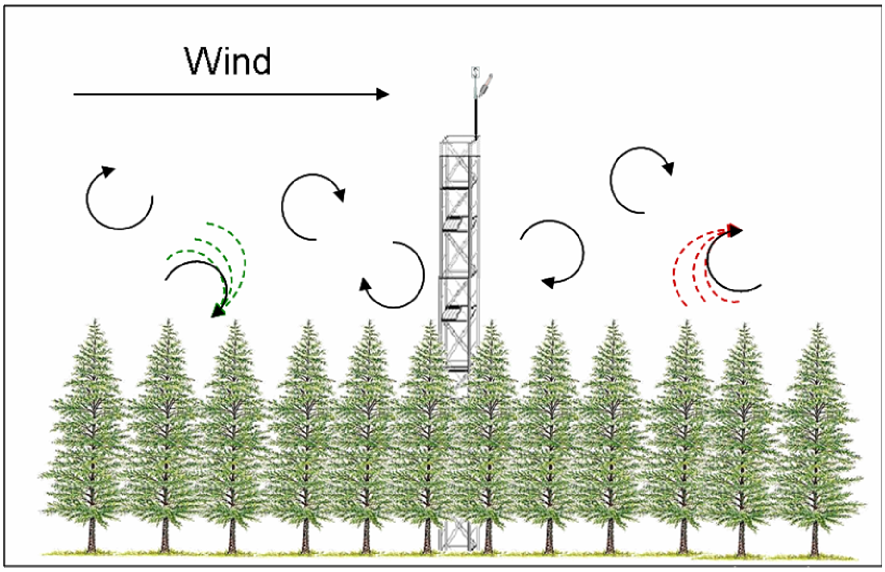


Figure 1.10: Simplified eddy covariance sketch (Modified. Burba & Anderson, 2007). Movement of air parcels above a forest canopy. Green arrows indicate $CO_2$ being extracted from the atmosphere while red arrows indicate a release of $CO_2$ to the atmosphere. The reproduction of the canopy is from Hecker (2006), reproduced with permission of the publisher BLV-Munich.

The sketch in Fig. 1.10 visualises the simplified eddy covariance scheme. Air in the canopy becomes $CO_2$ depleted by photosynthesis and $CO_2$ enriched by respiration. The rotating eddies exchange air in the canopy with air above the canopy during their chaotic motion. Thus at any point at a reference height the $CO_2$ concentration fluctuates around a mean value. These turbulent eddies have 3D components, including a vertical wind component (Burba & Anderson, 2007). It is by multiplying concentration by vertical wind speed that the components $\omega\rho_c$ are obtained. They travel across the forest and are recorded by the sonic anemometer, part of the eddy covariance system. Net horizontal fluxes are assumed to be zero when the site is large, homogeneous and on level ground.

The vertical component of wind velocity is derived from data provided by a three-axis sonic anemometer, while the carbon dioxide and water vapour concentrations are measured with a gas analyser. The eddy covariance (EC) setup in Harwood includes a closed path system, described in Jarvis (1995) and Moncrieff *et al.* (1997), which includes the fast response (20Hz) Li-6262 infra red gas analyser (IRGA) (LI-COR, Lincoln, NE, USA) which measures carbon dioxide ($CO_2$) and water vapour ($H_2O$) fluxes. This setup uses nitrogen ($N_2$) as a $CO_2/H_2O$ free reference gas, as a continuous flow through the reference cell. The ultrasonic anemometer is manufactured by Gill (Solent R3, Gill Instruments, Lymington, UK). Sample air is drawn through a Dekabon™ tube (Megaflex Ltd, Southwell, UK) and through the gas analyser by a diaphragm pump. This tubing is polythene on the inside, which is relatively non-absorbent to carbon dioxide and water vapour, protected by being inside an aluminium tube, and further protected on the outside by a tough plastic coat. The eddy covariance data was acquired with EdiSol, the software developed and written at the University of Edinburgh (Moncrieff *et al.*, 1997; Clement, 2004) and originally derived from EddySol (Jarvis, 1995). EdiSol calculates real-time fluxes of $CO_2$ and $H_2O$, as well as sensible ($H$) and latent heat ($\lambda E$), along with momentum and displays them in a user friendly way on a Laptop PC as part of the logging system. An impression of both systems is given in Fig. 1.11.

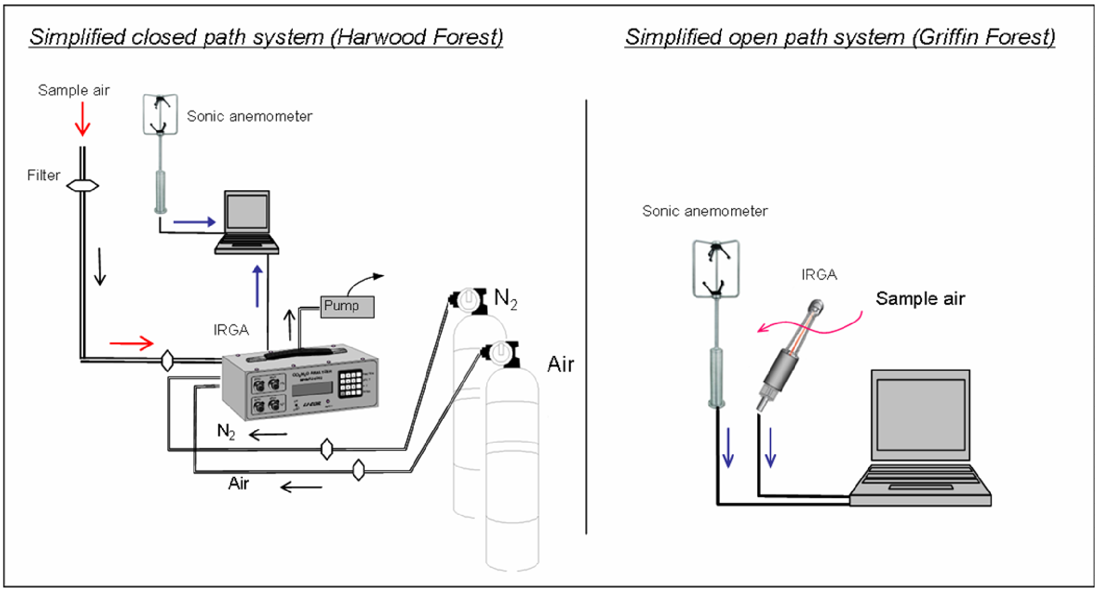


Figure 1.11: Simplified eddy covariance setup used in the current study. The closed path system is used in Harwood forest, where mains power is available. An open path system is used in Griffin forest (graphic: author's own).

The open path system we used at the second active forest site at Griffin (Clement, 2004) incorporates the Li-7500 IRGA (LI-COR, Lincoln, NE, USA). The advantage of this system is that it does not require any reference gases (apart from calibration purposes), also it is not dependent on a pump sucking air through the system, and it is not susceptible to problems of water and dirt in the tubing. When an air parcel moves through its infra-red beam, through its 3D measuring volume, then carbon and water vapour fluxes, momentum and other EC variables are determined instantaneously. Substantial corrections are however required, including especially the Webb-Pearmann-Leuning correction (Webb *et al.,* 1980; Burba *et al.,* 2006). The system is controlled via EdiSol in real-time and continuously logged on the site Laptop PC situated in the shed below the eddy flux tower.

As mentioned previously an ideal flux measurement site is a homogeneous forest on flat terrain (Baldocchi, 2003). An EC setup is not measuring $CO_2$ and $H_2O$ fluxes coming from the vicinity of the tower site, but from a zone further away. In order to measure the source of the air parcel, a footprint analysis (Baldocchi, 1997; Rannik *et al.,* 2000) is applied. This analysis makes it possible to estimate the source location by considering the time-averaged vertical flux of the air parcel at the top of the eddy flux tower to its turbulent diffusion from sources located upwind from the sonic anemometer and IRGA (Aubinet *et al.,* 2000). The size of the upwind fetch is dependent on wind direction and wind speed. Burba & Anderson (2007) simply describe the footprint as the area "seen" by the instrument located upwind, while fetch refers to the distance from the tower when describing the footprint area. Less homogeneous or too small forests lead to contamination of the carbon flux data with information from adjacent landscapes and also a significant horizontal flux. Detailed theoretical descriptions and further readings can be found in Baldocchi (1997); Aubinet *et al.* (2000); Rannik *et al.* (2000) and Markkanen *et al.* (2003).

Though we are using two different eddy covariance systems (open and closed path) (Haslwanter *et al.,* 2009), the same methodology applies. Raw data are processed with EdiRe, software developed and written at Edinburgh University (Clement,

2004) which applies various corrections derived from Leuning & Moncrieff (1990); Massman (2000); Massman & Lee (2002).

Gaps or spikes in data which happen during calibration or during downloading are filled by applying a simple linear regression, while larger gaps, due to power or equipment failure are treated and filled according to Carboeurope-IP guidelines. These guidelines in data gap filling are described and can be found in Falge *et al.* (2001) and Moffat *et al.* (2007).

### 1.4.5. Tree ring research

To examine the effects of diffuse radiation on growth, it is necessary to investigate long term tree growth patterns against a background of the interannual variability that reflects inherent seasonal variability of weather conditions over the years. In order to define this annual variability, meteorological data and tree ring information from nearby sites are used. Both Eskdalemuir and Ae are under maritime influences, and are not only remote but free from sources of major anthropogenic pollution. Eskdalemuir has the longest diffuse radiation records in the UK (Aeby, 2007).

Discs from stems of Sitka spruce [*Picea sitchensis (Bong.) Carr.*] (Fig. 1.12) were available from Forest of Ae (Dumfrieshire). Although Ae and Eskdalemuir are 25 km apart, they exibit the same changing weather patterns influenced by westerly and south westerly airflows, and large scale influences of atmospheric aerosol loading in the northern hemisphere.

The standardized methodology in tree ring research has been developed by dendrochronologists mainly for the reconstruction of summer temperatures (Schove, 1954; Spiecker, 1995; Briffa *et al.,* 1998; Kalela-Brundin, 1999; Gervais &

MacDonald, 2001; Briffa *et al.,* 2002) or precipitation (Spiecker, 1995) over the past centuries.

To investigate the interannual variability in tree growth, discs from Sitka spruce sections of mature stems (below 1 m) were used. 30 discs were provided by Forest Research, the research agency of the Forestry Commission, from Forest of Ae (Scotland). Prior to felling, North and West directions were marked on the bark, and the discs were frozen as soon as they were returned to the Forest Research station.

Discs were scanned on an A3 scanner and rings were counted in their frozen state using WinDendro (Version 2003a/b, Regent Instruments Inc., Quebec, Canada). This method enables an accurate measurement of the actual width, often ignored when using dried discs or tree cores which tend to shrink and crack during the drying process and may be also differently affected by moisture content. None of the discs used in the final analysis showed anomalous growth patterns, such as branch development, injury marks or false rings which might have influenced the growth of the tree on its northern side. The north radius was measured, in order to avoid 'noise' caused by compression wood (east) or downwards slope extension compensation (west) wood. The southern radius was ignored as it may have been influenced by microclimatological variation caused by direct solar irradiance.

Tree rings increase over the first few years of growth and then decrease steadily towards the bark (Dinwoodie, 1962; Phipps, 1982), assuming no thinning or fertilization has interrupted the natural growth. This standard age trend was factored out by de-trending prior to analysis. This was done by (i) first removing data covering the first few years (the juvenile section) (ii) fitting a simple cubic spline to the remaining 45 ring width values. We found the cubic spline represented the age-related decline in ring width very well ($r^2 = 0.97$). The residuals were taken as representing the effect of climate signals on tree growth (henceforth called the Growth Index).

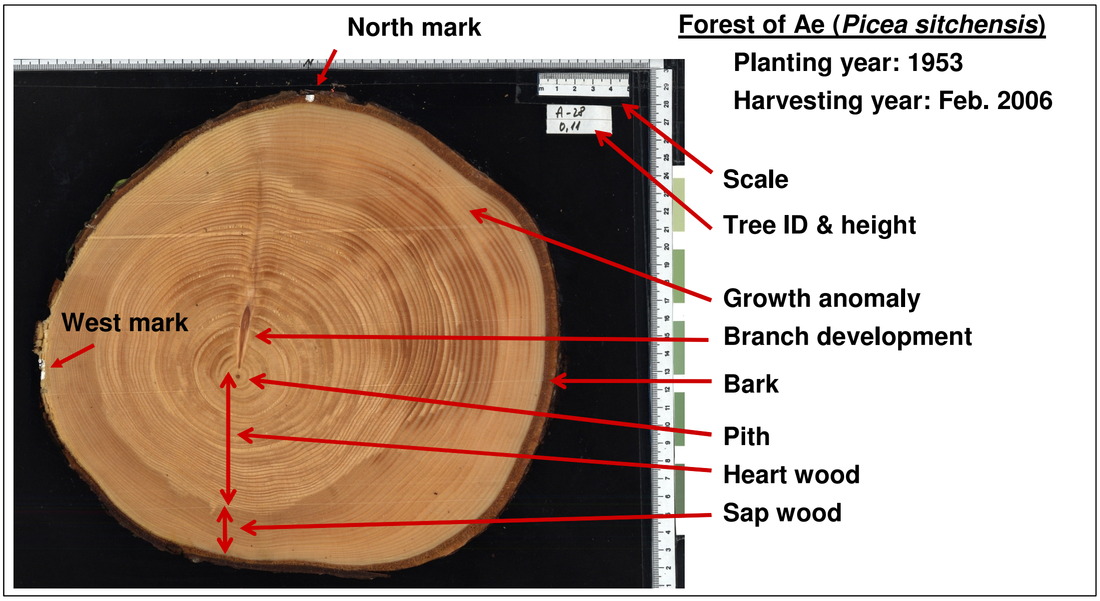


Figure 1.12: Freshly cut Sitka spruce [*Picea sitchensis (Bong.) Carr.*] tree disc. Tree felled in February 2006 in Forest of Ae.

## 1.5. Work plan and Structure of Thesis

The initial plan was to investigate the patterns of $CO_2$ uptake at two Sitka spruce plantations in northern Britain, relating the flux to variations in climatological data with a focus on the effect of diffuse versus direct radiation. After an initial setback (Appendix I), caused by the (accidental) and untimely felling of the research plot, a further line of research was incorporated: the exploration of possible long term effects of diffuse radiation on growth of this species.

Three of the chapters are written in the style of papers for submission to journals, and are referred to as Paper I, II and III. The steps in this research are as follows:

Chapter 2

Paper I - Influence of Clouds on the Solar Radiation Distribution in a Coniferous Forest.

We compared the amount and spectral distribution of direct and diffuse solar radiation above, within and below the forest canopy in order to investigate the different radiation fields above, within and below the canopy under various sky conditions. We show evidence that diffuse photosynthetic active radiation (PAR) is penetrating the canopy to a greater extent compared to direct PAR. Furthermore, results show a more favourable light quality for photosynthetic activity when the radiation field is diffuse.

## Chapter 3

### Paper II - $CO_2$ Exchange and Canopy Conductance of Coniferous Forests Under Various Sky Conditions.

It has been established carbon dioxide ($CO_2$) uptake by forest ecosystems is enhanced under diffuse skylight. We chose several days of eddy covariance (EC) and meteorological data recorded over the 2008 growing season in two Sitka spruce forests and divided them into the similar sky conditions as already introduced in **paper I**. The aim was to investigate the light response of photosynthesis under these diverse sky conditions and to study the relationship between different sky conditions (sunny/clear, cloudy and overcast) and canopy stomatal conductance ($g_c$). We found that Sitka spruce forests utilise radiation in a more efficient way under diffuse radiation. Furthermore, our results show a distinctive effect of diffuse radiation on the canopy stomatal conductance $g_c$.

## Chapter 4

### Paper III - A Relationship between Atmospheric Conditions and Tree Rings.

The growth of trees depends on a number of climatological variables (**paper I & paper II**). An integration of short term and long term studies serves the investigation of the possible link of climatological variables, such as diffuse radiation and forest growth, over several decades in northern Britain. We found a surprising high correlation between Sitka spruce tree rings and galactic cosmic radiation, which itself has a positive, albeit controversial, influence on cloud cover and diffuse radiation. Furthermore, we could establish a relationship between the fraction of solar radiation that is diffuse and volcanic eruptions upwind (west) to the UK.

## Chapter 5

## General discussion, Conclusions and Recommendations

In this chapter we re-iterate the main findings, discuss them together and suggest lines for further research.

## Chapter 6

## Appendix

## 1.6. References

Anonymous (1909) Eskdalemuir Observatory. *Nature* **81** (15 July), 86-86.

Aeby D (2007) Changes in Solar Irradiation at four Stations in the British Isles. *MSc Thesis*. University of Edinburgh. 72 pp.

Aubinet M, Grelle A et al. (2000) Estimates of the Annual Net Carbon and Water Exchange of Forests: The EUROFLUX Methodology. In *Advances in Ecological Research*. 113-175.

Bakan S (1978) Note on the eddy correlation method for $CO_2$ flux measurements. *Boundary-Layer Meteorology* **14**, 597-600.

Baldocchi DD (1997) Flux Footprints Within and Over Forest Canopies. *Boundary-Layer Meteorology* **85**, 273-292.

Baldocchi DD (2003) Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biology* **9**, 479-492.

Baldocchi DD, Hicks BB, Meyers TP (1988) Measuring Biosphere-Atmosphere Exchanges of Biologically Related Gases with Micrometeorological Methods. *Ecology* **69**, 1331-1340.

Ball T, Smith K, Moncrieff JB (2007) Effect of stand age on greenhouse gas fluxes from a Sitka spruce [*Picea sitchensis (Bong.) Carr.*] chronosequence on a peaty gley soil. *Global Change Biology* **13**, 2128-2142.

Briffa KR, Osborn TJ, Schweingruber FH, Jones PD, Shiyatov SG, Vaganov EA (2002) Tree-ring width and density data around the Northern Hemisphere: Part 1, local and regional climate signals. *The Holocene* **12**, 737-757.

Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Shiyatov SG, Vaganov EA (1998) Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature* **391**, 678-682.

Burba GG, Anderson DJ, Xu L, McDermitt DK (2006) Additional Term in the Webb-Pearman-Leuning Correction due to Surface Heating From an Open-Path Gas Analyzer. *Proceedings of American Geophysical Union*, Fall Meeting, San Francisco, California.

Burba GG, Anderson DJ (2007) Introduction to the Eddy Covariance Method: General Guidelines and Conventional Workflow. *LI-COR Biosciences*, http://www.licor.com, 141 pp.

Byrne AK, Green C (2004) The role of forests in the global carbon cycle and in climate change policy. *Irish Forestry* **61**, 7 - 15.

Calbo J, Gonzalez J-A, Pagegrave SD (2001) A Method for Sky-Condition Classification from Ground-Based Solar Radiation Measurements. *Journal of Applied Meteorology* **40**, 2193-2199.

Capers RS, Chazdon RL (2004) Rapid assessment of understory light availability in a wet tropical forest. *Agricultural and Forest Meteorology* **123**, 177-185.

Charlock TP, Sellers WD (1980) Aerosol, Cloud Reflectivity and Climate. *Journal of the Atmospheric Sciences* **37**, 1136-1138.

Chazdon RL, Pearcy RW (1991) The Importance of Sunflecks for Forest Understory Plants. *BioScience* **41**, 760-766.

Chen JM (1996a) Canopy architecture and remote sensing of the fraction of photosynthetically active radiation absorbed by boreal conifer forests. *Geoscience and Remote Sensing, IEEE Transactions on* **34**, 1353-1368.

Chen JM (1996b) Optically-based methods for measuring seasonal variation of leaf area index in boreal conifer stands. *Agricultural and Forest Meteorology* **80**, 135-163.

Chen JM, Blanken PD, Black TA, Guilbeault M, Chen S (1997) Radiation regime and canopy architecture in a boreal aspen forest. *Agricultural and Forest Meteorology* **86**, 107-125.

Chen JM, Cihlar J (1995) Quantifying the effect of canopy architecture on optical measurements of leaf area index using two gap size analysis methods. *Geoscience and Remote Sensing, IEEE Transactions on* **33**, 777-787.

Chen JM, Rich PM, Gower ST, Norman JM, Plummer S (1997) Leaf area index of boreal forests: Theory, techniques, and measurements. *Journal of Geophysical Research-Atmospheres* **102**, 29429-29443.

Chen J-C, Yang C-M, Wu S-T, Chung Y-L, Charles AL, Chen C-T (2007) Leaf Chlorophyll Content and Surface Spectral Reflectance of Tree Species along a Terrain Gradient in Taiwan's Kenting National Park. *Botanical Studies* **84**, 71-77.

Clement R (2004) Mass and Energy Exchange of a Plantation Forest in Scotland Using Micrometeorological Methods. *PhD Thesis*. University of Edinburgh, 416 pp.

Clement R, Moncrieff JB, Jarvis PG (2003) Net carbon productivity of Sitka Spruce forest in Scotland. *Scottish Forestry* **57**, 5-10.

Cohan DS, Xu J, Greenwald R, Bergin MH, Chameides WL (2002) Impact of atmospheric aerosol light scattering and absorption on terrestrial net primary productivity. *Global Biochemical Cycles* **16(4)**, 12pp.

Combes D, Sinoquet H, Varlet-Grancher C (2000) Preliminary measurement and simulation of the spatial distribution of the Morphogenetically Active Radiation (MAR) within an isolated tree canopy. *Annals of Forest Science* **57**, 497-511.

Cowan IR (1968) The Interception and Absorption of Radiation in Plant Stands. *Journal of Applied Ecology* **5**, 367-379.

Creber GT (1977) Tree Rings: A Natural Data-Storage System. *Biological Reviews* **52**, 349-381.

Dawson IK (2005) Eskdalemuir Observatory. *Weather* **60**, 66-69.

Desjardins RL, Lemon ER (1974) Limitations of an eddy-correlation technique for the determination of the carbon dioxide and sensible heat fluxes. *Boundary-Layer Meteorology* **5**, 475-488.

Dinwoodie JM (1962) Some Ring-width Pattern in Sitka Spruce Timber from North America. *Forestry* 35, 22-26.

Duchon CE, O'Malley MS (1999) Estimating cloud type from pyranometer observations. *Journal of Applied Meteorology* **38**, 132-141.

Endler JA (1993) The Color of Light in Forests and Its Implications. *Ecological Monographs* **63**, 1-27.

Fabian P (2002) Leben im Treibhaus : unser Klimasystem - und was wir daraus machen. Springer-Verlag, Berlin, 23-43 (258 pp).

Falconer RE (1965) A Simple Method for Obtaining a Continupus Record of Presence and Type of Clouds in Sky During Day. *Pure and Applied Geophysics* **60**, 236-244.

Falge E, Baldocchi DD et al. (2001) Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agricultural and Forest Meteorology* **107**, 43-69.

Farquhar GD, Roderick ML (2003) Atmospheric science: Pinatubo, diffuse light, and the carbon cycle. *Science* **299**, 1997-1998.

Federer CA, Tanner CB (1966) Spectral Distribution of Light in Forest. *Ecology* **47**, 555-560.

Fogwill F (2005) Field Guide for the GER 1500 - Single Beam Mode. NERC Field Spectroscopy Facility http://fsf.nerc.ac.uk.

Frazer GW, Canham CD, Lertzman KP (1999) Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-color fisheye photographs. Copyright 1999: Simon Fraser University, Burnaby, BC, and the Institute of Ecosystem Studies, Millbrook, New York.

Freedman JM, Fitzjarrald DR, Moore KE, Sakai RK (2001) Boundary layer clouds and vegetation-atmosphere feedbacks. *Journal of Climate* **14**, 180-197.

Fritts HC (1976) Tree rings and climate. Academic Press London, New York, 567 pp.

Fritts HC (1991) Reconstructing large-scale climatic patterns from tree-ring data: a diagnostic analysis. University of Arizona Press Tucson, 286 pp.

Gates D (1980) Biophysical ecology. Springer-Verlag New York, 611 pp.

Gendron F, Christian M, Ernest L, Philip GC (2006) The angular distribution of diffuse photosynthetically active radiation under different sky conditions in the open and within deciduous and conifer forest stands of Quebec and British Columbia, Canada. *Annals of Forest Science* **63**, 43-53.

Gervais BR, MacDonald GM (2001) Tree-ring and summer-temperature response to volcanic aerosol forcing at the northern tree-line, Kola Peninsula, Russia. *The Holocene* **11**, 499-505.

Goodale CL, Apps MJ et al. (2002) Forest Carbon Sinks in the Northern Hemisphere. *Ecological Applications* **12**, 891-899.

Gower ST, Kucharik CJ, Norman JM (1999) Characterization of radiation regimes in nonrandom forest canopies: theory, measurements, and a simplified modeling approach. *Tree Physiology* **19**, 695-706.

Grace J (2004) Understanding and managing the global carbon cycle. *Journal of Ecology* **92**, 189-202.

Grace J, Woolhouse HW (1973) A Physiological and Mathematical Study of the Growth and Productivity of a *Calluna-sphagnum* Community. II. Light Interception and Photosynthesis in Calluna. *Journal of Applied Ecology* **10**, 63-76.

Grant R (1997) Partitioning of biologically active radiation in plant canopies. *International Journal of Biometeorology* **40**, 26-40.

Gu L, Baldocchi DD, Wofsy SC, Munger JW, Michalsky JJ, Urbanski SP, Boden TA (2003) Response of a Deciduous Forest to the Mount Pinatubo Eruption: Enhanced Photosynthesis. *Science* **299**, 2035-2038.

Gu L, Baldocchi DD, Verma SB, Black TA, Vesala T, Falge EM, Dowty PR (2002) Advantages of diffuse radiation for terrestrial ecosystem productivity. *Journal of Geophysical Research* **107**.

Gu L, Fuentes JD, Shugart HH, Staebler RM, Black TA (1999) Responses of net ecosystem exchanges of carbon dioxide to changes in cloudiness: Results from two North American deciduous forests. *Journal of Geophysical Research* **104**, D24, 31,421-31,434.

Hale SE (2001) Light regime beneath Sitka spruce plantations in northern Britain: preliminary results. *Forest Ecology and Management* **151**, 61-66.

Hale SE (2003) The effect of thinning intensity on the below-canopy light environment in a Sitka spruce plantation. *Forest Ecology and Management* **179**, 341-349.

Hardy JP, Melloh R, Koenig G, Marks D, Winstral A, Pomeroy JW, Link T (2004) Solar radiation transmission through conifer canopies. *Agricultural and Forest Meteorology* **126**, 257-270.

Harrison RG, Chalmers N, Hogan RJ (2008) Retrospective cloud determinations from surface solar radiation measurements. *Atmospheric Research* **90**, 54-62.

Haslwanter A, Hammerle A, Wohlfahrt G (2009) Open-path vs. closed-path eddy covariance measurements of the net ecosystem carbon dioxide and water vapour exchange: A long-term perspective. *Agricultural and Forest Meteorology* **149**, 291-302.

Haurwitz B (1948) Insolation in Relation to Cloud Type. *Journal of Meteorology* **5**, 110-113.

Hecker U (2006) BLV-Handbuch Bäume und Sträucher. BLV: München, pp 479 (p69).

Inoue A, Yamamoto K, Mizoue N, Kawahara Y (2004) Effects of image quality, size and camera type on forest light environment estimates using digital hemispherical photography. *Agricultural and Forest Meteorology* **126**, 89-97.

Iqbal M (1983) An introduction to solar radiation. Academic Press Toronto, London, 390 pp.

Jarvis PG (1975) Water transfer in plants. In Heat and mass transfer in the biosphere. de Vries DA & van Alfen NK (ed.), Scripta Book Co., Washington, D.C, 369–394.

Jarvis PG (1995) The role of temperate trees and forests in $CO_2$ fixation. *Plant Ecology* **121**, 157-174.

Jonckheere I, Fleck S, Nackaerts K, Muys B, Coppin P, Weiss M, Baret F (2004) Review of methods for in situ leaf area index determination - Part I. Theories, sensors and hemispherical photography. *Agricultural and Forest Meteorology* **121**, 19-35.

Kalela-Brundin M (1999) Climatic information from tree-rings of Pinus sylvestris L. and a reconstruction of summer temperatures back to AD 1500 in Femundsmarka, eastern Norway, using partial least squares regression (PLS) analysis. *The Holocene* **9**, 59-77.

Kirkby J (2007) Cosmic Rays and Climate. *Surveys in Geophysics* **28**, 333-375.

Kurachi N, Hagihara A, Hozumi K (1993) Canopy photosynthetic production in a Japanese larch forest. II. Estimation of the canopy photosynthetic production. *Ecological Research* **8**, 349-361.

Leakey ADB, Press MC, Scholes JD (2003a) High-temperature inhibition of photosynthesis is greater under sunflecks than uniform irradiance in a tropical rain forest tree seedling. *Plant, Cell & Environment* **26**, 1681-1690.

Leakey ADB, Press MC, Scholes JD (2003b) Patterns of dynamic irradiance affect the photosynthetic capacity and growth of dipterocarp tree seedlings. *Oecologia* **135**, 184-193.

Leblanc SG (2008) DHP-TRACWin Manual. *Natural Resources Canada*, Canada Centre for Remote Sensing. Version 1.0.1.

Leblanc SG, Chen JM, Fernandes R, Deering DW, Conley A (2005) Methodology comparison for canopy structure parameters extraction from digital hemispherical photography in boreal forests. *Agricultural and Forest Meteorology* **129**, 187-207.

Leblanc SG, Chen, JM, Kwong M (2002) Tracing Radiation and Architecture of Canopies. TRAC Manual Version 2.1 27. *Natural Resources Canada*, Canada Centre for Remote Sensing.

Letts MG, Lafleur PM, Roulet NT (2005) On the relationship between cloudiness and net ecosystem carbon dioxide exchange in a peatland ecosystem. *Ecoscience* **12**, 53-59.

Leuning R, Moncrieff JB (1990) Eddy-covariance $CO_2$ flux measurements using open- and closed-path CO2 analysers: Corrections for analyser water vapour sensitivity and damping of fluctuations in air sampling tubes. *Boundary-Layer Meteorology* **53**, 63-76.

Lewandowska M, Hart JW, Jarvis PG (1977) Photosynthetic Electron Transport in Shoots of Sitka Spruce from Different Levels in a Forest Canopy. *Physiologia Plantarum* **41**, 124-128.

Li X, Strahler AH (1988) Modeling the gap probability of a discontinuous vegetation canopy. *Geoscience and Remote Sensing, IEEE Transactions on* **26**, 161-170.

Lohmann U, Feichter J (2005) Global indirect aerosol effects: a review. *Atmospheric Chemistry and Physics* **5**, 715-737.

MacArthur A (2006) Field Guide for the GER 1500 - Single Beam Mode. NERC Field Spectroscopy Facility, http://fsf.nerc.ac.uk.

MacArthur A (2007) Field Guide for the GER 1500 - Dual Beam Mode: Bi-Conical and Cos-Conical. NERC Field Spectroscopy Facility, http://fsf.nerc.ac.uk.

MacLellan C (2006) Guidelines for Post Processing GER 1500 Spectral Data Files using a FSF Excel Template. NERC Field Spectroscopy Facility, http://fsf.nerc.ac.uk.

Mann JE, Curry GL (1977) A sunfleck theory for general foliage location distributions. *Journal of Mathematical Biology* **5**, 87-97.

Markkanen T, Rannik Ü, Marcolla B, Cescatti A, Vesala T (2003) Footprints and Fetches for Fluxes over Forest Canopies with Varying Structure and Density. *Boundary-Layer Meteorology* **106**, 437-459.

Massman WJ (2000) A simple method for estimating frequency response corrections for eddy covariance systems. *Agricultural and Forest Meteorology* **104**, 185-198.

Massman WJ, Lee X (2002) Eddy covariance flux corrections and uncertainties in long-term studies of carbon and energy exchanges. *Agricultural and Forest Meteorology* **113,** 121-144.

Meir P, Cox P, Grace J (2006) The influence of terrestrial ecosystems on climate. *Trends in Ecology & Evolution* **21**, 254-260.

Mercado LM, Bellouin N, Sitch S, Boucher O, Huntingford C, Wild M, Cox PM (2009) Impact of changes in diffuse radiation on the global land carbon sink. *Nature* **458**, 1014-1017.

Milton EJ, Schaepman ME, Anderson K, Kneubühler M, Fox N (2009) Progress in field spectroscopy. *Remote Sensing of Environment* **113**, 92-109.

Min Q (2005) Impacts of aerosols and clouds on forest-atmosphere carbon exchange. *Journal of Geophysical Research* **110**, 12 pp.

Mochan S, Gardiner B (2007) Timber Properties of Sitka Spruce from South Scotland: a study to identify causes of increased failure during stress grading. *Forest Research Internal report*.

Moffat AM, Papale D et al. (2007) Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes. *Agricultural and Forest Meteorology* **147**, 209-232.

Moncrieff JB, Massheder JM et al. (1997) A system to measure surface fluxes of momentum, sensible heat, water vapour and carbon dioxide. *Journal of Hydrology* **188-189**, 589-611.

Monsi M, Saeki T (2005) On the Factor Light in Plant Communities and its Importance for Matter Production. *Annals of Botany* 95, 549-567. Orig. 1953, Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion, *Japanese Journal of Botany* 14, 22-52.

Monteith J, Unsworth MH (2008) Principles of Environamental Physics. Academic Press Amsterdam, 418 pp.

Morgan DC, Smith H (1978) Simulated sunflecks have large, rapid effects on plant stem extension. *Nature* **273**, 534-536.

Morgan DC, Warrington IJ, Rook DA (1985) Some observations on the spectral distribution characteristics of short-wave radiation within *Pinus radiata D. Don* canopies. *Plant, Cell and Environment* **8**, 201-206.

Muller RA (1971) Transmission components of solar radiation in pine stands in relation to climatic and stand variables. *Pacific Southwest Forest & Range Experiment Station, Forest Service, U.S. Department of Agriculture*; 13 pp.

Muneer T, Kubie J, Wood J (2007) Evaluation of a new photodiode sensor for measuring global and diffuse irradiance, and sunshine duration. *ASME Journal of Solar Energy Engineering* **125** (1). 1-6.

Ni W, Li X, Woodcock CE, Roujean J-L, Davis RE (1997) Transmission of solar radiation in boreal conifer forests: Measurements and models. *Journal of Geophysical Research* **102**.

Nichol CJ, Lloyd J, Shibistova O, Arneth A, Roeser C, Knohl A, Matsubara S, Grace J (2002) Remote sensing of photosynthetic-light-use efficiency of a Siberian boreal forest. *Tellus* **B 54**, 677-687.

Niyogi D, Chang H-I, Saxana VK et al. (2004) Direct observations of the effects of aerosol loading on net ecosystem $CO_2$ exchanges over different landscapes. *Geophysical Research Letters* **31**, 5pp

Norman JM, Jarvis PG (1974) Photosynthesis in Sitka Spruce (*Picea sitchensis (Bong.) Carr.*). III. Measurements of Canopy Structure and Interception of Radiation. *Journal of Applied Ecology* **11**, 375-398.

Norman JM, Jarvis PG (1975) Photosynthesis in Sitka Spruce (*Picea sitchensis (Bong.) Carr.*): V. Radiation Penetration Theory and a Test Case. *Journal of Applied Ecology* **12**, 839-878.

Pearcy RW (1990) Sunflecks and Photosynthesis in Plant Canopies. *Annual Review of Plant Physiology and Plant Molecular Biology* **41**, 421-453.

Pellatt MG, Mathewes RW (1997) Holocene Tree Line and Climate Change on the Queen Charlotte Islands, Canada. *Quaternary Research* **48**, 88-99.

Perry TO, Sellers HE, Blanchard CO (1969) Estimation of Photosynthetically Active Radiation Under a Forest Canopy With Chlorophyll Extracts and From Basal Area Measurements. *Ecology* **50**, 39-44.

Phipps RL (1982) Comments on Interpretation of Climatic Information from Tree Rings Eastern North America. *Tree-Ring Bulletin* **42**, 11-22.

Priestley CHB, Swinbank WC (1947) Vertical Transport of Heat by Turbulence in the Atmosphere. *Proceedings of the Royal Society of London*. Series A, Mathematical and Physical Sciences 189, 543-561.

Privette JL, Myneni RB, Knyazikhin Y, Mukelabai M, Roberts G, Tian Y, Wang Y Leblanc SG (2002) Early spatial and temporal validation of MODIS LAI product in the Southern Africa Kalahari. *Remote Sensing of Environment* **83**, 232–243.

Rannik Ü, Aubinet M, Kurbanmuradov O, Sabelfeld KK, Markkanen T, Vesala T (2000) Footprint Analysis For Measurements Over A Heterogeneous Forest. *Boundary-Layer Meteorology* **97**, 137-166.

Roderick M, Farquhar G, Berry S, Noble I (2001) On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. *Oecologia* **129**, 21-30.

Ruimy A, Jarvis P, Baldocchi DD, Saugier B (1995) $CO_2$ Fluxes over Plant Canopies and Solar Radiation: A Review. *Advances in Ecological Research* **26**.

Schimel DS (1995) Terrestrial ecosystems and the carbon cycle. *Global Change Biology* **1**, 77-91.

Schove DJ (1954) Summer Temperatures and Tree-Rings in North-Scandinavia A. D. 1461-1950. *Geografiska Annaler* **36**, 40-80.

Schweingruber FH (1988) Tree rings : basics and applications of dendrochronology. Kluwer Academic Publishers, Dordrecht, Boston, 276 pp.

Sellers PJ (1985) Canopy reflectance, photosynthesis and transpiration. *International Journal of Remote Sensing* **6**, 1335 - 1372.

Sinclair TR, Knoerr KR (1982) Distribution of Photosynthetically Active Radiation in the Canopy of a Loblolly Pine Plantation. *Journal of Applied Ecology* **19**, 183-191.

Smith H (1982) Light Quality, Photoperception, and Plant Strategy. *Annual Review of Plant Physiology* **33**, 481-518.

Smith TM, Cramer WP, Dixon RK, Leemans R, Neilson RP, Solomon AM (1993) The global terrestrial carbon cycle. *Water, Air, & Soil Pollution* **70**, 19-37.

Smith WK, Knapp AK, Reiners WA (1989) Penumbral Effects on Sunlight Penetration in Plant Communities. *Ecology* **70**, 1603-1609.

Sonohat G, Balandier P, Ruchaud F (2004) Predicting solar radiation transmittance in the understory of even-aged coniferous stands in temperate forests. *Annals of Forest Science* **61**, 629-641.

Spiecker H (1995) Growth dynamics in a changing environment — long-term observations. *Plant and Soil* **168-169**, 555-561.

Spiecker H (1999) Overview of Recent Growth Trends in European Forests. *Water, Air, & Soil Pollution* **116**, 33-46.

Stenberg P (1995) Penumbra in within-shoot and between-shoot shading in conifers and its significance for photosynthesis. *Ecological Modelling* **77**, 215-231.

Still CJ, Riley WJ et al. (2009) Influence of clouds and diffuse radiation on ecosystem-atmosphere $CO_2$ and $CO^{18}O$ exchanges. *Journal of Geophysical Research* **114**.

Szeicz G (1974) Solar Radiation for Plant Growth. *Journal of Applied Ecology* **11(2)**, 617-636.

Szekielda K-H, Gobler C, Gross B, Moshary F, Ahmed S (2003) Spectral reflectance measurements of estuarine waters. *Ocean Dynamics* **53**, 98-102.

Taylor AH (1990) Disturbance and Persistence of Sitka Spruce (*Picea sitchensis (Bong.) Carr.)* in Coastal Forests of the Pacific Northwest, North America. *Journal of Biogeography* **17**, 47-58.

Urban O, Janous D et al. (2007) Ecophysiological controls over the net ecosystem exchange of mountain spruce stand. Comparison of the response in direct vs. diffuse solar radiation. *Global Change Biology* **13**, 157-168.

van Gardingen PR, Jackson GE, Hernandez-Daumas S, Russell G, Sharp L (1999) Leaf area index estimates obtained for clumped canopies using hemispherical photography. *Agricultural and Forest Meteorology* **94**, 243-257.

Walker P (2009) Guidelines for Post Processing GER 1500 Spectral Data Files using a FSF Excel Template. NERC Field Spectroscopy Facility. http://fsf.nerc.ac.uk.

Waring RH, Franklin JF (1979) Evergreen Coniferous Forests of the Pacific Northwest. *Science* **204**, 1380-1386.

Waring RH, Running SW (1998) Forest ecosystems. Analysis at Multiple Scale. 370 pp.

Warren SG, Hahn CJ, London J (1985) Simultaneous Occurrence of Different Cloud Types. *Journal of Applied Meteorology* **24**, 658-667.

Webb EK, Pearman GI, Leuning R (1980) Correction of flux measurements for density effects due to heat and water vapour transfer. *Quarterly Journal of the Royal Meteorological Society* **106**, 85-100.

Weischet W (1977) Einführung in die allgemeine Klimatologie: physikalische und meteorologische Grundlagen. Teubner-Verlag, Stuttgart, 276 pp.

Wood J, Muneer T, Kubie J (2003) Evaluation of a New Photodiode Sensor for Measuring Global and Diffuse Irradiance, and Sunshine Duration. *Journal of Solar Energy Engineering* **125**, 43-48.

Zerva A, Ball T, Smith KA, Mencuccini M (2005) Soil carbon dynamics in a Sitka spruce [*Picea sitchensis (Bong.) Carr*.] chronosequence on a peaty gley. *Forest Ecology and Management* **205**, 227-240.

# Chapter 2

## Paper I: Influence of Clouds on the Solar Radiation Distribution in a Spruce Forest

Sigrid Dengel[1,2], John Grace[1,2], Alasdair MacArthur[3]

[1] Institute of Atmospheric and Environmental Science, School of GeoSciences,
Crew Building, University of Edinburgh, EH9 3JN, UK
[2] NERC NCEO/Centre for Terrestrial Carbon Dynamics, Sheffield, UK
[3] NERC Field Spectroscopy Facility (FSF), School of GeoSciences, The Grant
Institute, University of Edinburgh, EH9 3JW, UK

## 2. Influence of Clouds on the Solar Radiation Distribution in a Spruce Forest

### 2.1. Abstract

We compared the quantity (amount) and quality (spectral distribution) of direct and diffuse radiation above, within and below a forest stand under sunny, cloudy and overcast conditions in a thinned Sitka spruce [*Picea sitchensis (Bong.) Carr*.] forest (28 years old, with an leaf area index of around 5).

We found that there is a distinctive difference between direct (sunny) and diffuse (cloudy and overcast) radiation conditions inside the stand. We show evidence that diffuse photosynthetic active radiation (PAR) is penetrating the canopy to a greater extent compared to sunny conditions. Results show an enriched blue light inside the forest canopy, known to influence stomatal opening; also higher red:far red (R:FR) ratios under diffuse conditions, which is known to influence extension growth and allometrics.

Key words: Diffuse radiation, spectral distribution, light quality, spruce,
light extinction coefficient.

## 2.2. Introduction

The incoming solar radiation reaching the Earth surface is influenced by clouds through absorption, transmission and reflection, determining the percentage of incoming radiation that appears at the Earth's surface as 'direct' or 'diffuse'. It is well known that diffuse radiation, over a certain range of irradiance, enhances photosynthesis of terrestrial vegetation (Gu *et al.,* 1999; Roderick *et al.,* 2001; Gu *et al.,* 2002; Farquhar & Roderick, 2003; Letts *et al.*, 2005; Min, 2005; Urban *et al.,* 2007; Mercado *et al.,* 2009). Direct solar radiation is strong enough to cause light saturation of photosynthesis and possibly photo-inhibition (Powles, 1984; Krause, 1988; Long & Humphries, 1994) at the top of the canopy whilst under-saturation often occurs within the canopy and under-storey region as a result of shading. We hypothesise that optimal photosynthetic activity of the canopy is achieved under diffuse radiation (cloudy) conditions. Diffuse light may penetrate throughout the canopy illuminating all the leaves to some extent and providing a more evenly distributed radiation field.

Pioneers like Monsi and Saeki (1953) were among the first to investigate light penetration through a plant canopy. The vertical profile of irradiance is approximated by the Beer-Lambert equation of light extinction, serving as the base of many transmission studies (Perry *et al.,* 1969; Grace & Woolhouse, 1973; Norman & Jarvis, 1974; Lewandowska *et al.,* 1977; Sinclair & Knoerr, 1982; Kurachi *et al.,* 1993; Serrano *et al.,* 2000; Hale, 2001; Hale, 2003; Sonohat *et al.,* 2004). However, the equation does not describe the complexity of the radiation field to which the leaves are exposed, neither the spatial, nor the temporal distribution, because the forest canopy is not homogeneous (Gholz *et al.,* 1991; Smith *et al.,* 1991; Vose *et al.,* 1995). The diffuse radiation inside a forest canopy includes the fraction scattered by the foliage itself as well as radiation transmitted through the leaves and through the many gaps (Muller, 1971; Lee, 1987; Grant, 1997).

Sunflecks - their size, shape and duration and radiation distribution depend on the orientation and inclination of leaves within the forest canopy as well as the position of the sun in the sky (Federer & Tanner, 1966; Norman & Jarvis, 1974; Pearcy, 1990; Chazdon & Pearcy, 1991; Endler, 1993; Grant, 1997; Hardy *et al.,* 2004) and are closely related to effective gas exchange and photosynthetic production (Sellers, 1985; Kurachi *et al.,* 1993).

The observation that diffuse light is utilised more effectively than direct sunlight (Urban *et al.,* 2007; Mercado *et al.,* 2009) poses a number of questions to be addressed in the present work. The first is, to what extent is it true that light is distributed more evenly throughout the canopy under cloudy conditions; the second is, to what extent are spectral differences important in the response; and the third is, how important are the gaps, especially the gaps arising from management interventions.

## 2.3. Site description and Methodology

Measurements were carried out in Griffin Forest (planted 1979 - 1983), Central Scotland (Clement *et al.*, 2003; Clement, 2004). The site was row thinned in 2004 by removing every 5th row of trees. In addition, trees have been felled selectively resulting in a 30% removal of the forest stand (Fig. 2.1). The planting distance is around 2 m, with approximately 11 m from any mid-thinning line to the next (approx 1667 trees/ha, after thinning). The mean diameter at breast height (DBH) is 37 cm, mean canopy height 18 m and the estimated leaf area index (LAI) is around 5. A 115 m-long transect crossing 10 sections of 1 thinned and 4 planted rows with a North-South alignment was established in order to measure below canopy radiation.

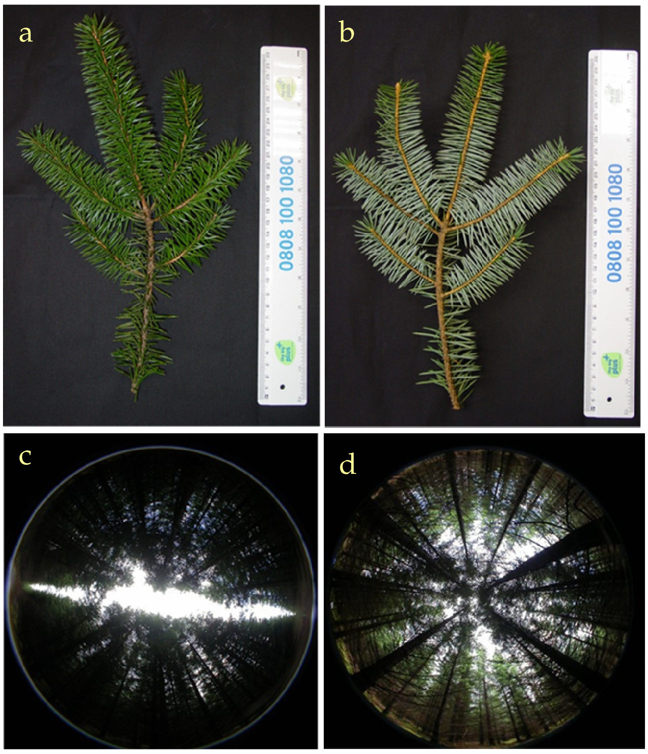


Figure 2.1: Sitka spruce [*Picea sitchensis (Bong.) Carr.*]. A Sitka spruce whorl seen from above (a) and below (b) as well as the canopy structure seen through a hemispherical lens. Visible are a distinctive thinning line (c) compared to a planted section (d) inside the forest.

The vertical and horizontal leaf area index (LAI) distribution was estimated from hemispherical images taken with a Nikon digital camera (Coolpix 4500, Nikon Corporation, Tokyo, Japan) with an attached fish eye lens (Fish-eye converter FC-E8, Nikon Corporation, Tokyo, Japan). Images are taken according to protocols used by Chen *et al.* (1997); van Gardingen *et al.* (1999); Inoue *et al.* (2004); Jonckheere *et al.* (2004) and are processed with the scientific image processing software Gap Light Analyzer (GLA) (Forest Renewal BC, Frazer S., 1999). When calculating LAI from hemispherical images in coniferous forests a correction value, known as the clumping index (van Gardingen *et al.,* 1999) is necessary to accommodate the structural aspects of the canopy (Fig. 2.1). The clumping index value has been calculated from several transect measurements in Griffin forest during the growing season 2007 and 2008 and was found to be 0.98.

For vertical LAI distribution along the tower we mounted the camera on a pole which was positioned away from the tower at various heights. Since the tower is obstructing each of these images, images were pre-processed prior to LAI analysis. All images have been halved to exclude the tower and then reconstructed by mirroring. This way we were able to estimate the vertical LAI distribution. All methods of LAI determination include stems. In deciduous trees the 'stem area index' is found during the leafless phase, whereas in evergreen trees this is not possible. Norman & Jarvis (1974) estimated the ratio between woody areas to the total to be 0.23 for the same species. No correction for stem was made.

Radiation penetration was measured using two spectroradiometers (GER1500, Spectra Vista, New York, USA), both fitted with cosine diffusers, permitting comparison of spectral photon flux in the canopy with simultaneously measured light in an open area. In this case, the 'open' site was above the canopy, on a 22 m scaffolding tower, and measurements were made at intervals through the canopy. The GER1500 instruments have a sampling resolution of 1.5 nm over the spectral range of 350 - 1050 nm. The spectral resolution is 3 nm which is recorded over 512 channels. The effective spectral resolution can be somewhat increased by applying post-processing methods, described in Walker (2009).

This band width includes parts of the ultra-violet (300 - 380 nm), the visible light (380 - 750 nm) and parts of the far and near infra-red bands (750 - 1050 nm).

All spectral measurements were undertaken following set protocols around solar noon (± 1h) during the summer of 2008. Tower and transect scans were undertaken on the same day within 30 min of each other. Several scans were performed at each metre along the tower (vertical profile), while the scans recorded for the horizontal gradient were measured at 2.5 metre intervals along the transect. Recordings were carried out under (i) clear conditions, (ii) altostratus (As) cloudy conditions and (iii) on an overcast day with a stratocumulus (Sc) cloud cover. In all cases light conditions did not change significantly over the measuring period.

Values of photosynthetically active radiation (PAR) were calculated by adjusting irradiant energy to quanta (μmol $m^{-2}s^{-1}$) and integrating from 400 - 700 nm (Bell *et al.,* 2000; Combes *et al.,* 2000):

$$PAR = \int_{\lambda=400}^{\lambda=700} Eh\upsilon(\delta\lambda) \tag{1}$$

where the limits of wavelength ($\lambda$) were 400 and 700 nm. Blue light (B) was calculated as:

$$B = \int_{430nm}^{460nm} Eh\upsilon(\delta\lambda) \tag{2}$$

where the limits of wavelength (λ) were 430 and 460 nm, which are within the margins of the blue light which evokes stomatal opening, described in Kuiper (1964); Mansfield & Meidner (1966); Sharkey & Raschke (1981); Zeiger & Field (1982); Karlsson (1986); Eisinger *et al.* (2000) and Briggs & Christie (2002). *E* is the spectral irradiance, *h* is the Planck constant and $\upsilon$ is frequency, given by $1/\lambda$. The wavelength increments used for the numerical integration were 1 nm.

The transmissivity of blue light ($\tau_{Sky}$ - eqn. 3) has been calculated as the ratio of B at the height *h* and B at 22 m (top of tower):

$$\tau_{Sky} = \frac{B_h}{B_{22}} \tag{3}$$

Herefrom we compared the blue transmisivity of the two diffuse conditions ($\tau_B$) and the blue light transmisivity on the clear day ($\tau_{Clear}$). These values were then used as an indication of blue light enrichment inside the forst canopy (eqn. 4):

$$\tau_B = \frac{\tau_{Sky}}{\tau_{Clear}} \tag{4}$$

For an indication of photomorphogenetic response, light quality may be stated as the red:far red (R:FR) ratio of incident radiation and expressed as (Heyward, 1984; Holmes & Smith, 1977):

$$\zeta = \frac{\int_{655nm}^{665nm} E_\lambda d\lambda}{\int_{725nm}^{735nm} E_\lambda d\lambda} \tag{5}$$

where $E_\lambda$ is the spectral irradiance (eqn 5). Holmes & Smith (1977) note that $\zeta$ (R:FR) remains more or less constant over the year and during the day, whereas within the canopy it is additionally dependent on the interaction of the light beam with photoelements.

Below-canopy PAR was also measured with a mobile handheld TRAC (Tracing Radiation and the Architecture of Canopies - Leblanc *et al.*, 2002) (3rd Wave Engineering, Nepean, CND) device, recording continuously at 32 Hz frequency along the same transect, resulting in a high resolution data set (> 50,000 data points per transect, about 175 per metre). It gives incoming total, diffuse and reflected (off the ground) PAR values, but also calculates LAI, *f*APAR, gap fraction and gap dimension. These measurements were made near solar noon. The sensor was manually moved along the transect. The standard walking pace while continuously recording is 0.3 m $s^{-1}$ in order to ensure a high resolution data set. Methods and theory description can be found in Chen & Cihlar (1995); Leblanc *et al.* (2002); Privette *et al.* (2002); Leblanc *et al.* (2005) and Leblanc (2008).

## 2.4. Results

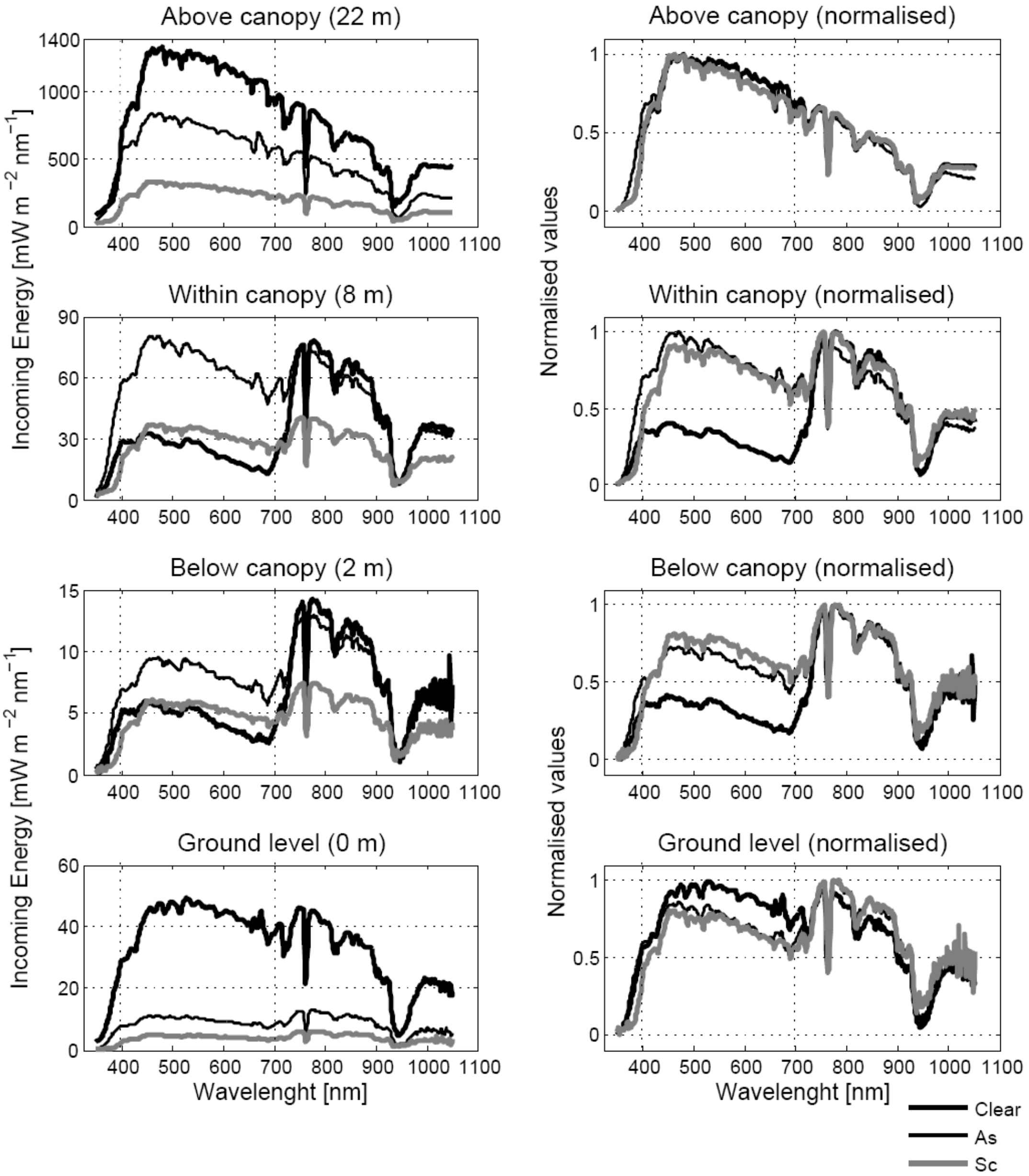


Figure 2.2: Spectra recorded above, within and below canopy (left panel) and their normalised values right panels. The three spectra correspond to three sky conditions (see key, lower right).

Fig. 2.2 (left panel) enables comparison of the spectra above (22 m) and within the canopy at 8 m, 2 m and at ground level. In Fig. 2.2(right panel) the data are normalised to their minima and maxima to make comparison of spectra easier. The incoming radiation does not differ much between the sky-types. All spectra of incoming radiation show the expected features: they have their peak spectral irradiances in the blue region at around 480 nm; both oxygen absorption bands are clearly seen (687 and 761 nm), and so are the large water absorption bands at around 730 and 940 nm.

Within the canopy (8 m) some important differences are seen between the sky-types. Under both cloudy conditions there is relatively more ultraviolet and blue radiation and relatively more radiation in the red and far-red regions of the spectrum. Much less of the incoming radiation is received from 400 to 750 nm in the case of the clear sky compared with the cloudy conditions. We may conclude that the upper part of the canopy has absorbed a large fraction of the incoming PAR. There are some differences between the spectra of the cloud types: the radiation from altostratus has relatively more energy in the visible and particularly in the shorter wavelengths (Fig. 2.6b). Below the canopy, at 2 m, these differences persist (Fig. 2.6b). However, at ground level we have recorded unexpectedly high irradiances under clear skies, enriched in the region of 500-700 nm. There is also an observed distinct steep increase in the far-red on clear days leading to similar values in the near infrared to cloudy and overcast days. Both cloudy scenarios show around 4 times more blue light inside the canopy compared to the clear sky scenario (Fig. 2.3).

The spectra were numerically integrated between 400 and 700 nm to yield values of PAR. Above the canopy on top of the 22 metre tall tower PAR was approximately 1600 µmol $m^{-2}$ $s^{-1}$ on the sunny day, 1000 µmol $m^{-2}$ $s^{-1}$ in altostratus, As and 400 µmol $m^{-2}$ $s^{-1}$ under stratocumulus, Sc. The mean PAR and LAI distributions down the vertical profile and the transmissivity ($\tau$) values associated with them are shown as attenuation curves in Figs 2.4(a), 2.4(b) and 2.4(c) respectively. The attenuation of direct radiation (‘clear’) is rapid at first (13-16 m), and then the location of the sensor happened to coincide with a sunfleck, which has produced a very high signal.

Under cloudy conditions the curves are relatively smooth, showing gradual attenuation on passing through the canopy.

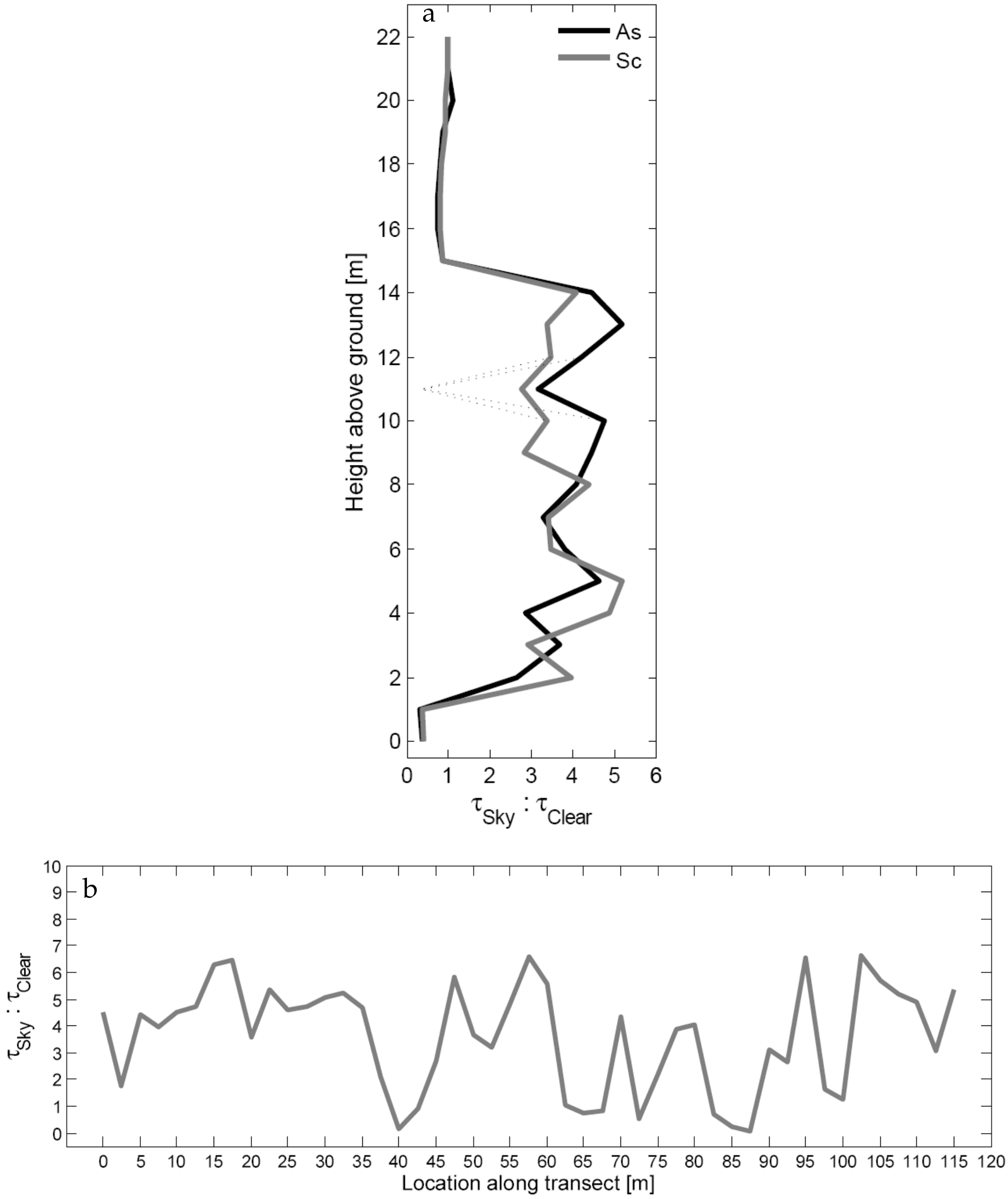


Figure 2.3: Ratio between Blue light transmissivity under various cloudy conditions and blue light transmissivity on the sunny day. (a) represents the ratio along the vertical profile. The thick black line represents the Altostratus sky type, while the thick grey line represents the overcast conditions. Both are shown after the sunfleck as been removed. Thin dotted line shows the distribution when sunfleck data is included. (b) represents the ratio along the transect for the overcast condition.

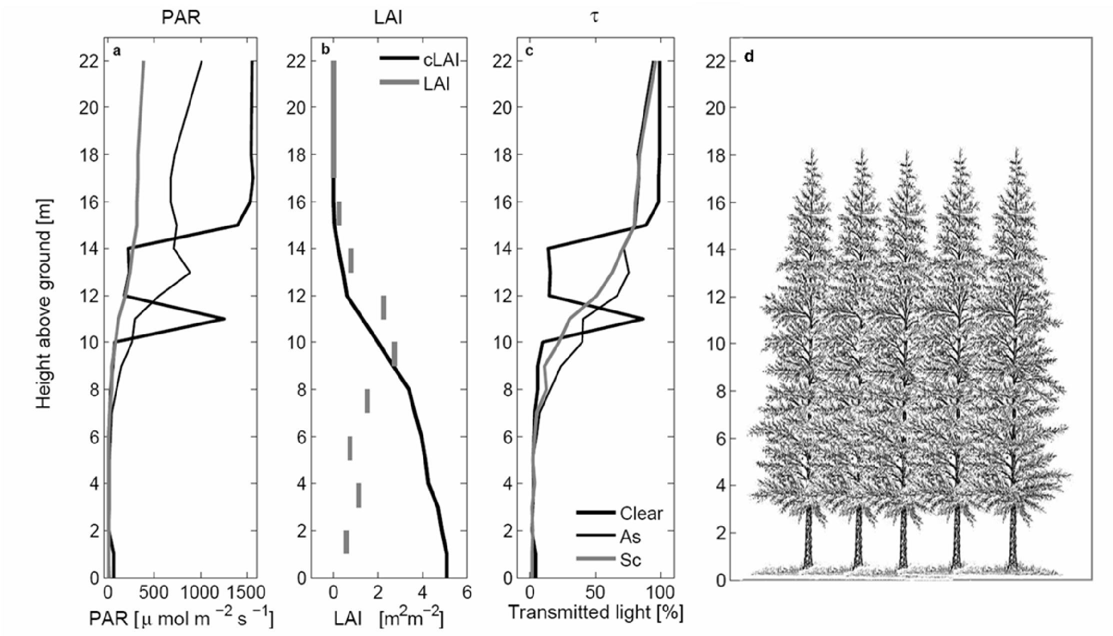


Figure 2.4: Radiation and transmissivity distribution - Griffin forest. Photosynthetic active radiation (PAR) along vertical profile (a) recorded under three different sky conditions: clear sky (‘Clear’), Altostratus cloud cover (‘As’) and under overcast conditions with Stratocumulus clouds (‘Sc’). Leaf area index (LAI) in successive 2 m bands and cumulative LAI (cLAI) (b) and the calculated transmissivity (c) along profile. 22 m indicates the top of the tower. Canopy height is approx 18 metres (d). The reproduction of the canopy is from Hecker (2006), reproduced with permission of the publisher BLV-Munich.

These data may be presented as a classical Beer-Lambert log-plot, wherein the slope may be used to yield the attenuation coefficient (*k*). In this case the classical Beer-Lambert approach applied only to diffuse conditions as seen in Fig. 2.5-B and 2.5-C with coefficient values of 0.8 and 0.7 respectively. Under sunny conditions this approach is unsuitable due to the inhomogeneous vertical distribution of foliage and the very high radiation attenuation within the upper canopy layer, resulting in *k* being 1.2.

Under sunny conditions the Beer-Lambert log-plot cannot be represented by a single straight line (Fig. 2.5-A1-A3). Overall, the result shows that under sunny conditions a very high fraction of PAR is absorbed or reflected at the top of the canopy, and therefore much less remains after a leaf area index of 1.5 (in the main canopy).

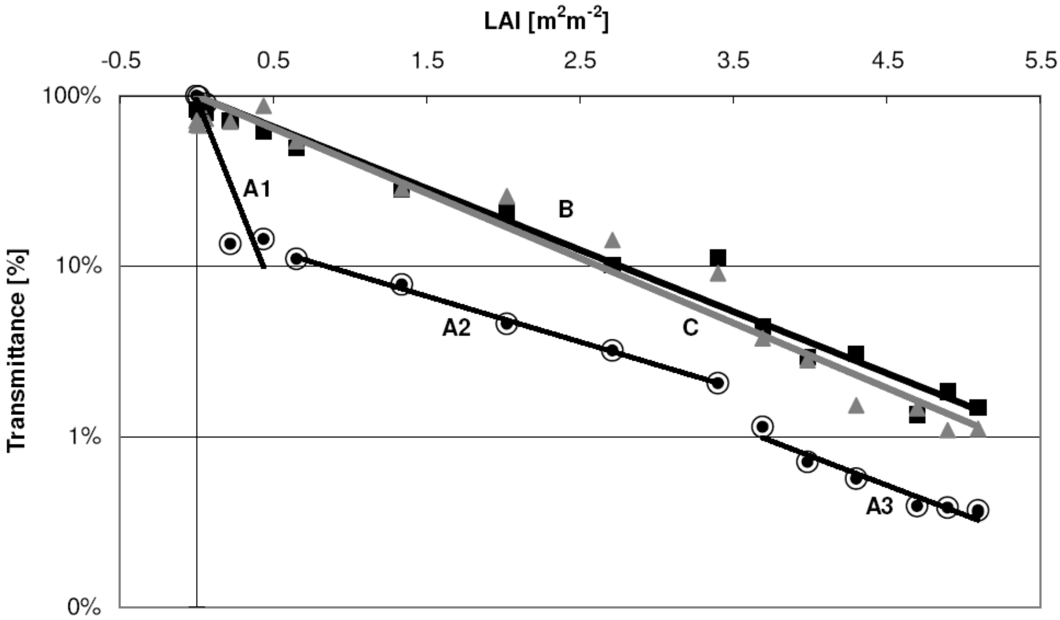


Figure 2.5: Transmissivity and attenuation curve according to the Monsi & Saeki (1953) method. Transmissivity and light attenuation through the forest canopy after applying the Beer-Lambert attenuation law. Grey triangles (B) represent As data, black squares represent Sc data and black dots and circles represent clear sky conditions. Values of the attenuation coefficient *k* extracted from Fig. 2.5 are shown in Table 2.1.

| Sky type | Canopy part | *k* (dimensionless) | r$^2$ |
|---|---|---|---|
| Altostratus | all | 0.87 | 0.96 |
| Stratocumulus | all | 0.79 | 0.98 |
| Clear | all * | 1.19 | 0.89 |
|  | top canopy | 5.2 | 0.82 |
|  | main canopy | 0.61 | 0.99 |
|  | below canopy | 0.79 | 0.93 |

Table 2.1: Values of the attenuation coefficient (k), extracted from Fig.2.5. * fitted Beer-Lambert curve not shown on graph.

The horizontal heterogeneity at the forest floor was surveyed, first by using the spectroradiometer, and performing the numerical integration as described above to obtain PAR. The distribution of transmitted PAR along the forest floor shows clearly the thinning lines, and indicates that there is more diffuse PAR reaching the forest floor (Fig. 2.6b). Direct sunflecks could not be recorded during these measurements (they are very short-lived and often missed during point measurements along transects). However, a very bright region was observed around the 85th m (Fig. 2.5a & b). Such features occur in areas where several neighbouring trees are missing due to row and selective thinning within a very small spatial area. Additional measurements along this transect were done with the TRAC sensor, and, due to the high spatial resolution, they show a very high occurrence of sunflecks (Fig. 2.7).

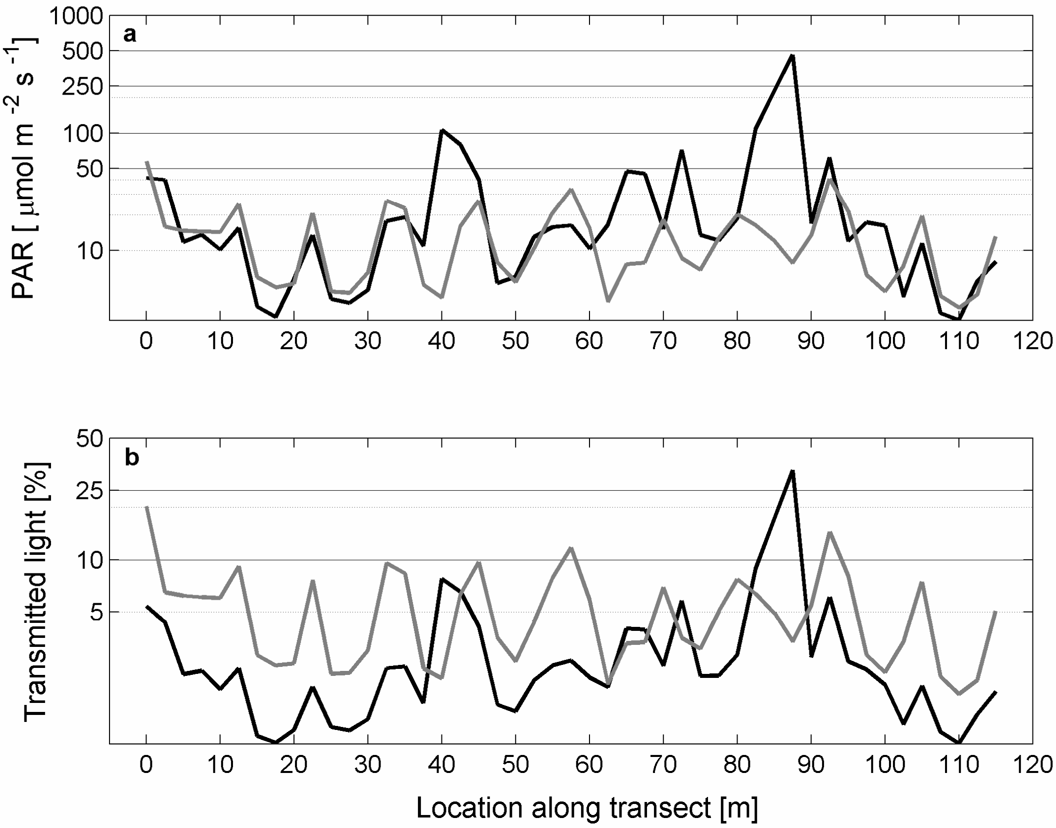


Figure 2.6: Distribution of photosynthetic active radiation (PAR) along a 115 m long transect. Horizontal distribution of PAR measured along the transect (a) and the transmittance (b).
Measurements have been done only on a clear (black bold line) and under overcast conditions with Stratocumulus clouds, shown in grey.

Measurements with the TRAC device were carried out on several occasions. For the current study only those days representative for our investigation (same or similar above-canopy incoming radiation) have been chosen. For presentation, two representative days per sky condition are displayed. In clear-sky conditions the huge variation caused by sunflecks is seen (Fig. 2.7), often reaching several hundred µmol of photons $m^{-2}$ $s^{-1}$, superimposed on a background that varies systematically according to the presence of thinning rows, from a minimum of about 3 to a maximum of about 20 µmol $m^{-2}$ $s^{-1}$ . Cloudy conditions (Fig. 2.8) show highly regular behaviour, closely resembling the 'background' values shown in the previous Figure, although about 50% higher.

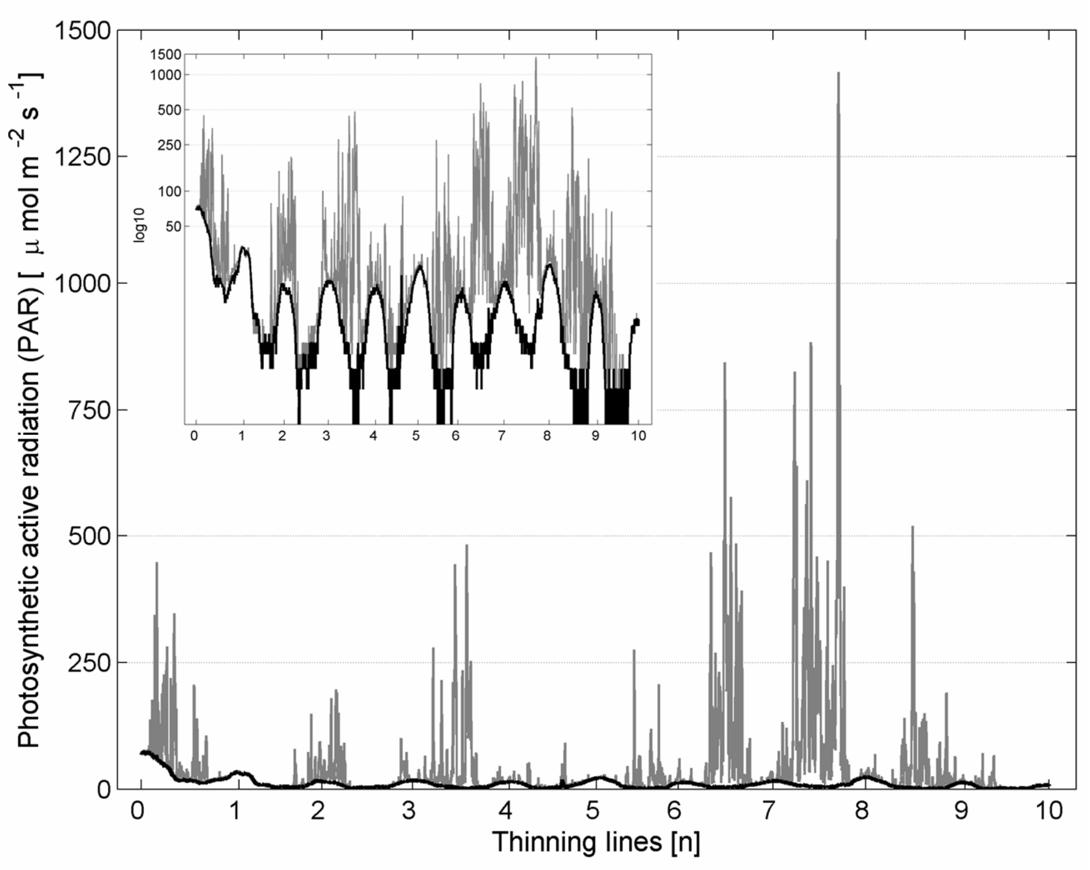


Figure 2.7: Below canopy PAR measurements under sunny conditions. Measurements were carried out on a clear sky day (see main text). Global radiation is marked with a bold grey line (diffuse radiation = global radiation - direct radiation). The black bold line is the diffuse component measured simultaneously. TRAC has a shading strip in order to keep direct sunlight out of the 'diffuse' sensor head. The insert graph has been reproduced with a logarithmic scale for clarity.

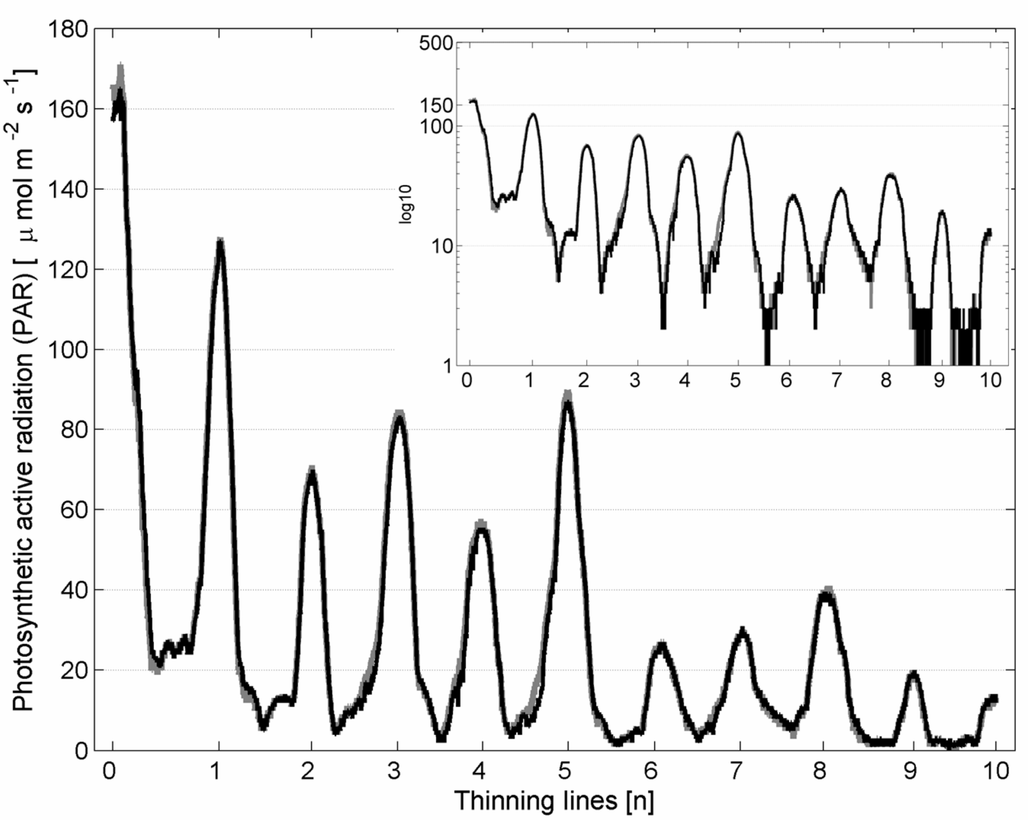


Figure 2.8: Radiation distribution under overcast conditions. Measurements were carried out on an overcast day (see main text). The bold grey line, just visible, shows the global and the black bold line illustrates the diffuse component. The insert graph has been reproduced with a logarithmic scale for clarity.

TRAC data from four days were accumulated into 'bins' of 5% transmittance classes to investigate the frequency distributions of irradiances according to class (Fig. 2.9). The data are presented on a logarithmic scale to make comparison easier. The clear and cloudy data form two distinct patterns. In the case of 'clear', 95% of the measurements show a penetration through the canopy of only 0-5%; whereas in the 'overcast' case, 95% of the measurements show 0-20% penetration. We may conclude that diffuse radiation penetrates the canopy to a greater extent. High energy sunflecks are evident in the long 'tail' of the graph: but only 1.5% of all the measurements in direct sunlight fall in a penetration class of more than 50%.

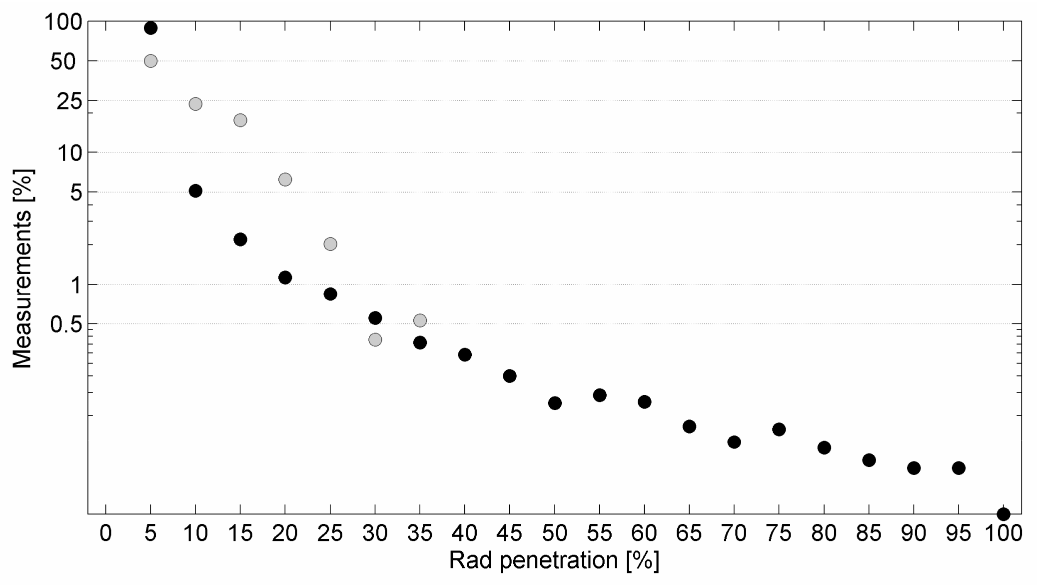


Figure 2.9: Classification of accumulated measurements, using TRAC. Data were accumulated and distributed into 5%-transmitttance classes. Black dots represent 'sunny' values while grey dots represent 'overcast' values.

Fig. 2.10a illustrates the red far-red ratio along the vertical gradient while Fig. 2.10b shows the results from the horizontal transect measurements. The ratio in the canopy shows a different pattern for clear skies than for cloudy skies. In clear conditions, there is a region of the canopy with very low red:far-red ratio, usually indicative of deep shade (Fig. 2.10a). However, there is a considerable spatial variation, as the horizontal data set shows (Fig. 2.10b). In large gaps, like the one at 40 m and 85 m, the clear-sky R:FR is high. Usually, however, it is low.

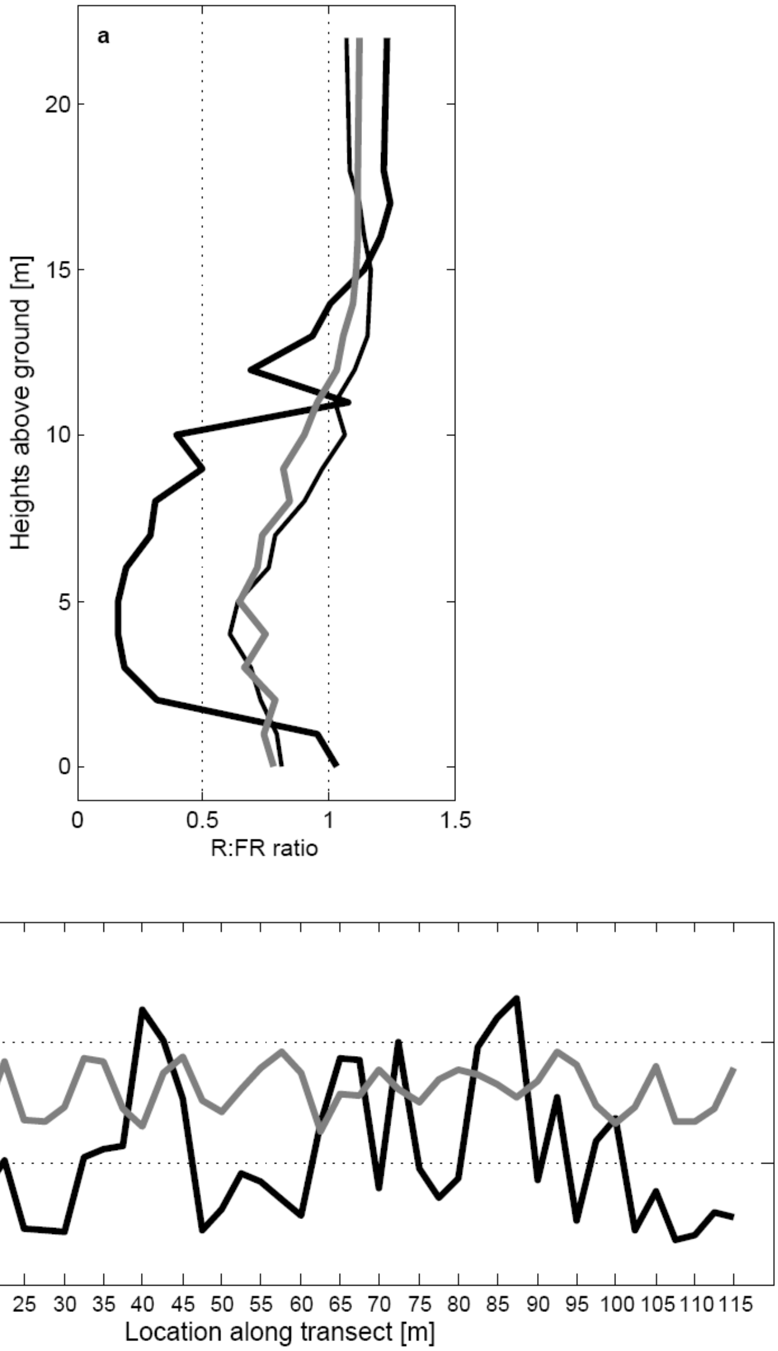


Figure 2.10: Vertical and horizontal distribution of light quality in a coniferous forest. Light quality (R:FR) measurements along the vertical profile (a) and horizontally along the transect (b). Clear sky conditions are represented in a thick black line, the thick black line represents the As data set while bold grey lines represent the overcast conditions.

## 2.5. Discussion

### 2.5.1. Contrasting light attenuation under cloudy versus clear skies

It is evident that there are profound differences in the transmissivity of solar radiation from the different sky conditions. The most important of these is the extent to which the direct sunlight is absorbed or reflected near the top of the canopy, shown by the attenuation patterns (Figs 2.3 & 2.4) and is therefore not available for photosynthesis lower down in the canopy. It is also shown, quite independently, by the extent to which the diffuse radiation is relatively more enhanced at the forest floor (Fig. 2.6) and by the distribution of ground-level data between transmission classes (Fig. 2.9). This general feature was also shown by Morgan *et al.* (1985) for pine canopies and more recently by Leuchner *et al.* (2005); Navratil *et al.* (2007) and Urban *et al.* (2007) for Norway spruce. The vertical profile we describe may suffer from bias, because it is a single location measurement (close to the tower), yet the ground measurements, which do represent a large spatial sample, show consistent results.

The vertical profile under sunny conditions demonstrates only a poor fit to the Beer-Lambert Law. There is identifiable variation in the calculated value of the attenuation coefficient *k*, as was also shown by Norman & Jarvis (1974) and Lewandowska *et al.* (1977), who obtained similar *k*-values to those reported here. We presume that the explanation of this variation lies in the variable structure as one proceeds from the top to the bottom of the canopy: near the top the leaves are densely crowded on the stems, whereas near the bottom leaves are thin, sparse and attenuation is dominated by braches and stems (Norman & Jarvis, 1974; Schulze *et al.,* 1977; Ford, 1982; Leverenz *et al.,* 1982; Stenberg *et al.,* 1998). This variation is illustrated by the hemispherical photographs (Fig. 2.1(c & d), where the image at ground level is dominated by woody tissue rather than leaves.

### 2.5.2. Gaps and sunflecks determine spatial patterns

Under clear skies the occurrences of gaps in the crown, which are sometimes short-lived and wind-dependent (Federer & Tanner, 1966; Pearcy, 1990; Chazdon & Pearcy, 1991), are spots where the direct radiation beam, or some fraction of it, penetrates into the canopy, sometimes as far as the forest floor (Stenberg, 1995). They create highly illuminated areas where the incident light can *in extremis* reach higher values than above the canopy itself due to a high proportion of scattering of radiation on the surrounding branches (Muller, 1971; Kueppers *et al.,* 1997). Sunfleck spectra are similar to incident radiation (Endler, 1993; Combes *et al.,* 2000; de Castro, 2000) and may also be areas with transient higher temperatures, which in some cases may have physiological significance. Sunflecks also have red:far-red (R:FR) ratios (Fig. 2.10) close to those measured above the canopy (Reitmayer *et al.,* 2001).

Leverenz & Jarvis (1979, 1980) determined light response curves of this species under controlled conditions and found saturation at around 500 µmol photons $m^{-2}s^{-1}$, a value which is often exceeded at the top of the canopy. If the uppermost level of canopy is experiencing an over-saturation of light and also encountering the highest shoot temperatures in the forest, it is possible that stress responses such as closure of stomata may occur (in this species stomata respond strongly to leaf-to-air vapour pressure difference in a self protective way (Grace *et al.,* 1975; Neilson & Jarvis, 1975; Alton *et al.,* 2007). Other stress responses such as photoinhibition are also possible (Powles, 1984; Krause, 1988; Long & Humphries, 1994). Thus, along the sunfleck-pathway, such effects may contribute to under-activity of photosynthesis in relation to the level of incident radiation (Pearcy, 1990).

At the forest floor a complex spatial pattern of sunflecks is seen (Fig. 2.6). The intensity of the sunflecks shows that almost always they are penumbral (i.e. they are nearly always less than they would be if the solar disc were visible, Stenberg, 1995). They appear not in the thinning lines but below the trees themselves: under clear sky conditions there is a lateral shift in the total penetrated radiation compared with the diffuse skies. This phenomenon is visible because the lines in this forest happen to be oriented East-West, and at the prevailing solar angles (max 10° (Dec) - max 56° (June)) the beam must pass through a large thickness of canopy in order to reach the ground.

### 2.5.3. Spectral effects

The spectral distribution of radiation is very important for plant growth and morphogenesis, (Endler, 1993; de Castro, 2000; Galen *et al.,* 2004; Escobar-Gutuiérrez *et al.,* 2009). The spectral distribution of incoming solar radiation was similar under all three sky conditions. However, substantially more energy in the photosynthetically active wavebands penetrated the canopy in the case of diffuse skies (Fig. 2.6). There was particularly more blue light (440-470 nm) within the canopy under cloudy skies (Fig. 2.2, Fig. 2.3), possibly a result of multiple reflections and scattering involving the waxy abaxial surfaces of needles (Fig. 2.1) (Jeffree *et al.,* 1971; Reicosky & Hanover, 1978; Cape & Percy, 1993). Blue-enrichment may have important implications for stomatal control. Morison & Jarvis (1983) reported that blue wavelengths are more effective in causing stomatal opening than red wavelengths while the opposite is the case for carbon dioxide assimilation. Smith (1982) reported that at low PAR stomata open only in response to blue, red light being ineffective; thus, if this is a general result, we may conclude that the conditions of diffuse radiation in the present case are especially conducive to stomatal opening in the lower regions of the canopy, where PAR is low in all three conditions.

As in most coniferous canopies, the light is only slightly green-enriched, compared with what is usual in broadleaved trees and herbaceous crops (Lichtenthaler *et al.,* 1996; Knapp & Carter, 1998).

This characteristic is partly the result of the large amount of stems which constitute the canopy, and partly because of the structure and orientation of the coniferous shoot and the needles they hold (Norman & Jarvis, 1974; Leverenz *et al.*, 1982). This structural aspect is clear from the hemispherical photographs in which rather little leaf is visible. In this species Norman & Jarvis (1974) estimated the ratio between stem and branches, as being the woody area, to the total canopy area including green and nongreen areas (Chen 1996a, 1996b) to be as high as 0.23.

Within the canopy there is a very high proportion of near infrared under all three sky conditions (Fig. 2.2). This is not surprising, as leaves generally transmit as much as 50% of incident radiation at this waveband and reflect much of the remaining (Middleton & Walter-Shea, 1995; Middleton *et al.*, 1997; Knapp & Carter, 1998; Combes *et al.*, 2000; Carter & Knapp, 2001). On the other hand, in the chlorophyll-absorbing region of the red, leaves transmit rather little energy; therefore, the ratio of red to far red is dictated by the presence of leaves. This aspect of light quality has received much attention. The decline (Fig. 2.10) in the red:far red (R:FR) has long been known and has been linked in numerous studies to aspects of photomorphogenesis (see reviews by Federer & Tanner, 1966; Smith, 1982; Morgan *et al.*, 1985; Endler, 1993; Smith & Whitelam, 1997; Lieffers *et al.*, 1999; Capers & Chazdon, 2004; Leuchner *et al.*, 2005; Pecot *et al.*, 2005; Wherley *et al.*, 2005; Chelle *et al.*, 2007; Leuchner *et al.*, 2007 and Navrátil *et al.*, 2007).

Smith (1982) indicates that the blue-absorbing photoreceptor acts to measure light quantity and that the pigment phytochrome can act to detect the red:far-red ratio (R:FR) as an indicator of light quality. This ratio also regulates important aspects of plant growth including stem elongation in plants (Smith, 1982; Corre, 1983; Ballare *et al.*, 1991; Assmann, 1992; de la Rosa *et al.*, 1998; Franklin & Whitelam, 2005; Pecot *et al.*, 2005; Wherley *et al.*, 2005).

Ritchie (1997) reported the ability of *Pseudotsuga menziesii* seedlings to detect the presence of nearby trees via changes in light quality and the ability to adjust their growth allometry. In particular, most researchers (Smith, 1982; Corre, 1983; Ballare *et al.,* 1991; Assmann, 1992; de la Rosa *et al.,* 1998; Franklin & Whitelam, 2005; Pecot *et al.,* 2005; Wherley *et al.,* 2005) find that low R:FR increases stem elongation , but also many other factors: growth rate, shape and, in the present case, this may have implications for the adjustment to light and competition, and the optimisation of branch location in the canopy. Furthermore, Kasperbauer (1971, 1987) showed that row spacing and orientation (in tobacco plants) are also important regarding light quality. Wherley *et al.* (2005) reported that high R:FR ratios promoted greater chlorophyll production in turfgrass by influencing phytochrome equilibrium. Leuchner *et al.* (2007) indicate that a reduction of the R:FR ratio is a strong indicator for competition. In the present study, we have found that the R:FR ratio in the canopy is much lower under clear skies, indicating a lower photomorphogenical 'light quality' (*sensu* Smith, 1982) than under diffuse conditions.

## 2.6. Conclusion

We showed that diffuse PAR is penetrating better through the forest canopy due to the ability of the forest to act as a neutral filter under diffuse conditions and also due to an increased scattering and reflection of the foliage itself. Below the active crown PAR appears very similar under all three conditions, though blue being more enriched under diffuse conditions, enhancing stomatal opening. It becomes clear that for the all-canopy photosynthesis diffuse PAR is preferred.

We further suggest that apart from having a vertical shift between direct and diffuse radiation inside forest canopies we are also experiencing a lateral shift in radiation under various conditions. Concluding, it can be said that depending on sky conditions we are experiencing not only a vertical shift in light quantity and light quality but also a lateral shift inside the canopy leading to a different photosynthetic response (see the next chapter)..

Furthermore, spectra recorded under these diverse conditions and influenced by associated spectral shifts due to absorption, reflectance or scattering inside the forest canopy leads to the conclusion that radiation inside the photosynthesising canopy caused by diffuse skies is qualitatively better than radiation inside the canopy under clear skies. We could show how the spectral distribution of radiation is changed by the foliage itself, and how trees are regulating their coexistence and achieve higher photosynthetic activity under diffuse cloudy and overcast conditions.

## 2.7. Acknowledgements

The Author would like to thank Anitra Fraser, who has spent hours on top of the tower supervising the above canopy measurements and synchronising hemispherical pictures taken of the sky. Furthermore we would like to thank Ciaran Beggan, Dr Axel Wellpot and Dr Salvador Hernandez-Daumas for their support during measuring campaigns along the tower and below the canopy. Futhermore the authors would like to thank Dr. Terry Dawson for providing the TRAC system, which has been frequently used. Last but not least we would like to thank the staff at the NERC Field Spectroscopy Facility (FSF) (Edinburgh) for their patience before field campaigns and with post-processing issues.

This study would not have happened without the project approval by NERC (National Environmental Research Council) and the loan of the paired spectrometer by the NERC FSF (Edinburgh).

## 2.8. References

Alton PB, North PN, Los SO (2007) The impact of diffuse sunlight on canopy light-use efficiency, gross photosynthetic product and net ecosystem exchange in three forest biomes. *Global Change Biology* **13**, 776-787.

Assmann SM (1992) Effects of light quantity and quality during development on the morphology and stomatal physiology of Commelina communis. *Oecologia* **92**, 188-195.

Ballaré CL, Scopel AL, Sánchez RA (1991) Photocontrol of stem elongation in plant neighbourhoods: effects of photon fluence rate under natural conditions of radiation. *Plant, Cell and Environment* **14**, 57-65.

Bell GE, Danneberger TK, McMahon MJ (2000) Spectral Irradiance Available for Turfgrass Growth in Sun and Shade. *Crop Science* **40**, 189-195.

Briggs WR, Christie JM (2002) Phototropins 1 and 2: versatile plant blue-light receptors. *Trends in Plant Science* **7**, 204-210.

Cape JN, Percy KE (1993) Environmental influences on the development of spruce needle cuticles. *New Phytologist* **125**, 787-799.

Capers RS, Chazdon RL (2004) Rapid assessment of understory light availability in a wet tropical forest. *Agricultural and Forest Meteorology* **123**, 177-185.

Carter GA, Knapp AK (2001) Leaf optical properties in higher plants: linking spectral characteristics to stress and chlorophyll concentration. *Americal Journal of Botany* **88**, 677-684.

Chazdon RL, Pearcy RW (1991) The Importance of Sunflecks for Forest Understory Plants. *BioScience* **41**, 760-766.

Chelle M, Evers JB, Combes D, Varlet-Grancher C, Vos J, Andrieu B (2007) Simulation of the three-dimensional distribution of the red:far-red ratio within crop canopies. *New Phytologist* **176**, 223-234.

Chen JM (1996a) Canopy architecture and remote sensing of the fraction of photosynthetically active radiation absorbed by boreal conifer forests. *Geoscience and Remote Sensing, IEEE Transactions on* **34**, 1353-1368.

Chen JM (1996b) Optically-based methods for measuring seasonal variation of leaf area index in boreal conifer stands. *Agricultural and Forest Meteorology* **80**, 135-163.

Chen JM, Blanken PD, Black TA, Guilbeault M, Chen S (1997) Radiation regime and canopy architecture in a boreal aspen forest. *Agricultural and Forest Meteorology* **86**, 107-125.

Chen JM, Cihlar J (1995) Quantifying the effect of canopy architecture on optical measurements of leaf area index using two gap size analysis methods. *Geoscience and Remote Sensing, IEEE Transactions on* **33**, 777-787.

Chen JM, Rich PM, Gower ST, Norman JM, Plummer S (1997) Leaf area index of boreal forests: Theory, techniques, and measurements. *Journal of Geophysical Research-Atmospheres* **102**, 29429-29443.

Clement R (2004) Mass and Energy Exchange of a Plantation Forest in Scotland Using Micrometeorological Methods. *PhD Thesis*. University of Edinburgh, 416 pp.

Clement R, Moncrieff JB, Jarvis PG (2003) Net carbon productivity of Sitka Spruce forest in Scotland. *Scottish Forestry* **57**, 5-10.

Combes D, Sinoquet H, Varlet-Grancher C (2000) Preliminary measurement and simulation of the spatial distribution of the Morphogenetically Active Radiation (MAR) within an isolated tree canopy. *Annals of Forest Science* **57**, 497-511.

Coombe DE (1957) The Spectral Composition of Shade Light in Woodlands. *Journal of Ecology* **45**, 823-830.

Corre W (1983) Growth and morphogenesis of sun and shade plants. II. The influence of light quality. *Acta Botanica Neerlandica* **32**, 185-202.

Cowan IR (1968) The Interception and Absorption of Radiation in Plant Stands. *Journal of Applied Ecology* **5**, 367-379.

de Castro F (2000) Light spectral composition in a tropical forest: measurements and model. *Tree Physiology* **20**, 49-56.

de la Rosa TM, Aphalo PJ, Lehto T (1998) Effects of far-red light on the growth, mycorrhizas and mineral nutrition of Scots pine seedlings. *Plant and Soil* **201**, 17-25.

Endler JA (1993) The Color of Light in Forests and Its Implications. *Ecological Monographs* **63**, 1-27.

Eisinger W, Swartz TE, Bogomolni RA, Taiz L (2000) The Ultraviolet Action Spectrum for Stomatal Opening in Broad Bean. *Plant Physiology* **122**, 99-106.

Escobar-Gutiérrez AJ, Combes D, Rakocevic M, de Berranger C, Eprinchard-Ciesla A, Sinoquet H, Varlet-Grancher C (2009) Functional relationships to estimate Morphogenetically Active Radiation (MAR) from PAR and solar broadband irradiance measurements: The case of a sorghum crop. *Agricultural and Forest Meteorology In Press*, Corrected Proof.

Farquhar GD, Roderick ML (2003) Atmospheric science: Pinatubo, diffuse light, and the carbon cycle. *Science* **299**, 1997-1998.

Federer CA, Tanner CB (1966) Spectral Distribution of Light in Forest. *Ecology* **47**, 555-560.

Ford ED (1982) High Productivity in a Polestage Sitka Spruce Stand and its Relation to Canopy Structure. *Forestry* **55**, 1-17.

Franklin KA, Whitelam GC (2005) Phytochromes and Shade-avoidance Responses in Plants. *Annals of Botany* **96**, 169-175.

Frazer GW, Canham CD, Lertzman KP (1999) Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-color fisheye photographs. Copyright 1999: Simon Fraser University, Burnaby, BC, and the Institute of Ecosystem Studies, Millbrook, New York.

Galen C, Huddle J, Liscum E (2004) An Experimental Test of the Adaptive Evolution of Phototropins: Blue-Light Photoreceptors Controlling Phototropism in *Arabidopsis thaliana*. *Evolution* **58**, 515-523.

Gholz HL, Vogel SA, Cropper WP, Jr., McKelvey K, Ewel KC, Teskey RO, Curran PJ (1991) Dynamics of Canopy Structure and Light Interception in *Pinus Elliottii* Stands, North Florida. *Ecological Monographs* **61**, 33-51.

Grace J, Woolhouse HW (1973) A Physiological and Mathematical Study of the Growth and Productivity of a *Calluna-sphagnum* Community. II. Light Interception and Photosynthesis in Calluna. *Journal of Applied Ecology* **10**, 63-76.

Grace J, Malcolm DC, Bradbury IK (1975) The Effect of Wind and Humidity on Leaf Diffusive Resistance in Sitka Spruce Seedlings. *The Journal of Applied Ecology* **12**, 931-940.

Grant R (1997) Partitioning of biologically active radiation in plant canopies. *International Journal of Biometeorology* **40**, 26-40.

Gu L, Baldocchi D, Verma SB, Black TA, Vesala T, Falge EM, Dowty PR (2002) Advantages of diffuse radiation for terrestrial ecosystem productivity. *Journal of Geophysical Research* **107**, 4050.

Gu L, Fuentes JD, Shugart HH, Staebler RM, Black TA (1999) Responses of net ecosystem exchanges of carbon dioxide to changes in cloudiness: Results from two North American deciduous forests. *Journal of Geophysical Research* **104**.

Hale SE (2001) Light regime beneath Sitka spruce plantations in northern Britain: preliminary results. *Forest Ecology and Management* **151**, 61-66.

Hale SE (2003) The effect of thinning intensity on the below-canopy light environment in a Sitka spruce plantation. *Forest Ecology and Management* **179**, 341-349.

Hardy JP, Melloh R, Koenig G, Marks D, Winstral A, Pomeroy JW, Link T (2004) Solar radiation transmission through conifer canopies. *Agricultural and Forest Meteorology* **126**, 257-270.

Hayward PM (1984) Determination of phytochrome parameters from radiation measurements. In: Smith, H., Holmes, M.G. (Eds.), Techniques in Photomorphogenesis. Academic Press London, 159–173.

Hecker U (2006) BLV-Handbuch Bäume und Sträucher. BLV: München, pp 479 (p69).

Holmes MG, Smith H (1977) The Function of Phytochrome in the Natural Environment IV. Light Quality and Plant Development. *Photochemistry and Photobiology* **25**, 551-557.

Inoue A, Yamamoto K, Mizoue N, Kawahara Y (2004) Effects of image quality, size and camera type on forest light environment estimates using digital hemispherical photography. *Agricultural and Forest Meteorology* **126**, 89-97.

Jeffree CE, Johnson RPC, Jarvis PG (1971) Epicuticular wax in the stomatal antechamber of sitka spruce and its effects on the diffusion of water vapour and carbon dioxide. *Planta* **98,** 1-10.

Jonckheere I, Fleck S, Nackaerts K, Muys B, Coppin P, Weiss M, Baret F (2004) Review of methods for in situ leaf area index determination - Part I. Theories, sensors and hemispherical photography. *Agricultural and Forest Meteorology* **121**, 19-35.

Karlsson PE (1986) Blue light regulation of stomata in wheat seedlings. II. Action spectrum and search for action dichroism. *Physiologia Plantarum* **66**, 207-210.

Kasperbauer MJ (1971) Spectral Distribution of Light in a Tobacco Canopy and Effects of End-of-Day Light Quality on Growth and Development. *Plant Physiology* **47**, 775-778.

Kasperbauer MJ (1987) Far-Red Light Reflection from Green Leaves and Effects on Phytochrome-Mediated Assimilate Partitioning under Field Conditions. *Plant Physiology* **85**, 350-354.

Knapp AK, Carter GA (1998) Variability in leaf optical properties among 26 species from a broad range of habitats. *Americal Journal of Botany* **85**, 940-946.

Krause GH (1988) Photoinhibition of photosynthesis. An evaluation of damaging and protective mechanisms. *Physiologia Plantarum* **74**, 566-574.

Kuiper PJC (1964) Dependence upon Wavelength of Stomatal Movement in Epidermal Tissue of Senecio odoris. *Plant Physiology* **39**, 952-955.

Kuppers M, Timm H, Orth F, Stegemann J, Stober R, Schneider H, Paliwal K, Karunaichamy KSTK, Ortiz R (1996) Effects of light environment and successional status on lightfleck use by understory trees of temperate and tropical forests. *Tree Physiology* **16**, 69-80.

Kurachi N, Hagihara A, Hozumi K (1993) Canopy photosynthetic production in a Japanese larch forest. II. Estimation of the canopy photosynthetic production. *Ecological Research* **8**, 349-361.

Leblanc SG (2008) DHP-TRACWin Manual. *Natural Resources Canada*, Canada Centre for Remote Sensing. Version 1.0.1.

Leblanc SG, Chen JM, Fernandes R, Deering DW, Conley A (2005) Methodology comparison for canopy structure parameters extraction from digital hemispherical photography in boreal forests. *Agricultural and Forest Meteorology* **129**, 187-207.

Leblanc SG, Chen, JM, Kwong M (2002) Tracing Radiation and Architecture of Canopies. TRAC Manual Version 2.1 27. *Natural Resources Canada*, Canada Centre for Remote Sensing.

Lee DW (1987) The Spectral Distribution of Radiation in Two Neotropical Rainforests. *Biotropica* **19**, 161-166.

Letts MG, Lafleur PM, Roulet NT (2005) On the relationship between cloudiness and net ecosystem carbon dioxide exchange in a peatland ecosystem. *Ecoscience* **12**, 53-59.

Leuchner M, Menzel A, Werner H (2007) Quantifying the relationship between light quality and light availability at different phenological stages within a mature mixed forest. *Agricultural and Forest Meteorology* **142**, 35-44.

Leuchner M, Fabian P, Werner H (2005) Spectral Multichannel Monitoring of Radiation within a Mature Mixed Forest. *Plant Biology* **7**, 619-627.

Leverenz J, Deans JD, Ford ED, Jarvis PG, Milne R, Whitehead D (1982) Systematic Spatial Variation of Stomatal Conductance in a Sitka Spruce Plantation. *Journal of Applied Ecology* **19**, 835-851.

Leverenz JW, Jarvis PG (1979) Photosynthesis in Sitka Spruce. VIII. The Effects of Light Flux Density and Direction on the Rate of Net Photosynthesis and the Stomatal Conductance of Needles. *Journal of Applied Ecology* **16**, 919-932.

Leverenz JW, Jarvis PG (1980) Photosynthesis in Sitka Spruce (Picea Sitchensis (Bong.) Carr.): X. Acclimation to Quantum Flux Density Within and Between Trees. *Journal of Applied Ecology* **17**, 697-708.

Lewandowska M, Hart JW, Jarvis PG (1977) Photosynthetic Electron Transport in Shoots of Sitka Spruce from Different Levels in a Forest Canopy. *Physiologia Plantarum* **41**, 124-128.

Lichtenthaler HK, Gitelson A, Lang M (1996) Non-destructive determination of chlorophyll content of leaves of a green and an aurea mutant of tobacco by reflectance measurements. *Journal of Plant Physiology* **148**, 483-493.

Lieffers VJ, Messier C, Stadt KJ, Gendron F, Comeau PG (1999) Predicting and managing light in the understory of boreal forests. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **29**, 796-811.

Long SP, Humphries S, Falkowski PG (1994) Photoinhibition of Photosynthesis in Nature. *Annual Review of Plant Physiology and Plant Molecular Biology* **45**, 633-662.

Mansfield TA, Meidner H (1966) Stomatal Opening in Light of Different Wavelengths: Effects of Blue Light Independent of Carbon Dioxide Concentration. *Journal of Experimental Botany* **17**, 510-521.

Mercado LM, Bellouin N, Sitch S, Boucher O, Huntingford C, Wild M, Cox PM (2009) Impact of changes in diffuse radiation on the global land carbon sink. *Nature* **458**, 1014-1017.

Middleton EM, Chan SS, Rusin RJ, Mitchell SK (1997) Optical properties of black spruce and jack pine needles at BOREAS sites in Saskatchewan, Canada. *Canadian Journal of Remote Sensing* **23**, 108-119.

Middleton EM, Walter-Shea EA (1995) Optical properties of canopy elements in the boreal forest. In Geoscience and Remote Sensing Symposium, 1995. *Quantitative Remote Sensing for Science and Applications* **1**, 789-793.

Min Q (2005) Impacts of aerosols and clouds on forest-atmosphere carbon exchange. *Journal of Geophysical Research* **110**.

Monsi M, Saeki T (2005) (orig. 1953) On the Factor Light in Plant Communities and its Importance for Matter Production. *Annals of Botany* **95**, 549-567.

Morgan DC, Smith H (1981) Control of Development in Chenopodium album L. By Shadelight: The Effect of Light Quantity (Total Fluence Rate) and Light Quality (Red: Far-Red Ratio). *New Phytologist* **88**, 239-248.

Morgan DC, Warrington IJ, Rook DA (1985) Some observations on the spectral distribution characteristics of short-wave radiation within *Pinus radiata* D. Don canopies. *Plant, Cell and Environment* **8**, 201-206.

Morison JIL, Jarvis PG (1983) Direct and Indirect Effects of Light on Stomata .1. in Scots Pine and Sitka Spruce. *Plant Cell and Environment* **6**, 95-101.

Muller RA (1971) Transmission components of solar radiation in pine stands in relation to climatic and stand variables. *Pacific Southwest Forest & Range Experiment Station, Forest Service, U.S. Department of Agriculture*; 13 pp.

Navrátil M, Špunda V, Marková I, Janouš D (2007) Spectral composition of photosynthetically active radiation penetrating into a Norway spruce canopy: the opposite dynamics of the blue/red spectral ratio during clear and overcast days. *Trees - Structure and Function* **21**, 311-320.

Neilson RE, Jarvis PG (1975) Photosynthesis in Sitka Spruce (*Picea-Sitchensis (Bong) Carr)* .VI. Response of Stomata to Temperature. *Journal of Applied Ecology* **12**, 879-891.

Ni W, Li X, Woodcock CE, Roujean J-L, Davis RE (1997) Transmission of solar radiation in boreal conifer forests: Measurements and models. *Journal of Geophysical Research* **102**.

Norman JM, Jarvis PG (1974) Photosynthesis in Sitka Spruce (*Picea sitchensis (Bong.) Carr.*). III. Measurements of Canopy Structure and Interception of Radiation. *Journal of Applied Ecology* **11**, 375-398.

Norman JM, Jarvis PG (1975) Photosynthesis in Sitka Spruce (*Picea sitchensis (Bong.) Carr.*): V. Radiation Penetration Theory and a Test Case. *Journal of Applied Ecology* **12**, 839-878.

Pearcy RW (1990) Sunflecks and Photosynthesis in Plant Canopies. *Annual Review of Plant Physiology and Plant Molecular Biology* **41**, 421-453.

Pecot SD, Horsley SB, Battaglia MA, Mitchell RJ (2005) The influence of canopy, sky condition, and solar angle on light quality in a longleaf pine woodland. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **35**, 1356-1366.

Perry TO, Sellers HE, Blanchard CO (1969) Estimation of Photosynthetically Active Radiation Under a Forest Canopy With Chlorophyll Extracts and From Basal Area Measurements. *Ecology* **50**, 39-44.

Powles SB (1984) Photoinhibition of Photosynthesis Induced by Visible Light. *Annual Review of Plant Physiology* **35**, 15-44.

Privette JL, Myneni RB, Knyazikhin Y, Mukelabai M, Roberts G, Tian Y, Wang Y, Leblanc SG (2002) Early spatial and temporal validation of MODIS LAI product in the Southern Africa Kalahari. *Remote Sensing of Environment* **83**, 232–243.

Reicosky DA, Hanover JW (1978) Physiological Effects of Surface Waxes: I. Light Reflectance for Glaucous and Nonglaucous *Picea pungens*. *Plant Physiology* **62**, 101-104.

Reitmayer H, Werner H, Fabian P (2002) A Novel System for Spectral Analysis of Solar Radiation within a Mixed Beech-Spruce Stand. *Plant Biology* **4**, 228-233.

Ritchie GA (1997) Evidence for red:far red signaling and photomorphogenic growth response in Douglas-fir (*Pseudotsuga menziesii*) seedlings. *Tree Physiology* **17**, 161-168.

Roderick M, Farquhar G, Berry S, Noble I (2001) On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. *Oecologia* **129**, 21-30.

Schulze ED, Fuchs MI, Fuchs M (1977) Spacial distribution of photosynthetic capacity and performance in a mountain spruce forest of Northern Germany. *Oecologia* **29**, 43-61.

Sellers PJ (1985) Canopy reflectance, photosynthesis and transpiration. *International Journal of Remote Sensing* **6**, 1335 - 1372.

Serrano L, Gamon JA, Peńuelas J (2000) Estimation of canopy photosynthetic and nonphotosynthetic components from spectral transmittance. *Ecology* **81(11)**, 3149-3162.

Sharkey TD, Raschke K (1981) Effect of Light Quality on Stomatal Opening in Leaves of Xanthium-Strumarium L. *Plant Physiology* **68**, 1170-1174.

Sinclair TR, Knoerr KR (1982) Distribution of Photosynthetically Active Radiation in the Canopy of a Loblolly Pine Plantation. *Journal of Applied Ecology* **19**, 183-191.

Smith FW, Sampson DA, Long JN (1991) Comparison of Leaf-Area Index Estimates from Tree Allometrics and Measured Light Interception. *Forest Science* **37**, 1682-1688.

Smith H (1982) Light Quality, Photoperception, and Plant Strategy. *Annual Review of Plant Physiology* **33**, 481-518.

Smith H, Whitelam GC (1997) The shade avoidance syndrome: multiple responses mediated by multiple phytochromes. *Plant, Cell and Environment* **20**, 840-844.

Sonohat G, Balandier P, Ruchaud F (2004) Predicting solar radiation transmittance in the understory of even-aged coniferous stands in temperate forests. *Annals of Forest Science* **61**, 629-641.

Stenberg P (1995) Penumbra in within-shoot and between-shoot shading in conifers and its significance for photosynthesis. *Ecological Modelling* **77**, 215-231.

Stenberg P, Smolander H, Sprugel D, Smolander S (1998) Shoot structure, light interception, and distribution of nitrogen in an Abies amabilis canopy. *Tree Physiology* **18**, 759-767.

Urban O, Janous D et al. (2007) Ecophysiological controls over the net ecosystem exchange of mountain spruce stand. Comparison of the response in direct vs. diffuse solar radiation. *Global Change Biology* **13**, 157-168.

van Gardingen PR, Jackson GE, Hernandez-Daumas S, Russell G, Sharp L (1999) Leaf area index estimates obtained for clumped canopies using hemispherical photography. *Agricultural and Forest Meteorology* **94**, 243-257.

Vose JM, Sullivan NH, Clinton BD, Bolstad PV (1995) Vertical Leaf-Area Distribution, Light Transmittance, and Application of the Beer-Lambert Law in 4 Mature Hardwood Stands in the Southern Appalachians. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **25**, 1036-1043.

Walker P (2009) Guidelines for Post Processing GER 1500 Spectral Data Files using a FSF Excel Template. NERC Field Spectroscopy Facility. http://fsf.nerc.ac.uk.

Wherley BG, Gardner DS, Metzger JD (2005) Tall Fescue Photomorphogenesis as Influenced by Changes in the Spectral Composition and Light Intensity. *Crop Science* **45**, 562-568.

Zeiger E, Field C (1982) Photocontrol of the Functional Coupling between Photosynthesis and Stomatal Conductance in the Intact Leaf: Blue Light and Par-Dependent Photosystems in Guard Cells. *Plant Physiology* **70**, 370-375.

# Chapter 3

## Paper II: $CO_2$ Exchange and Canopy Conductance of Coniferous Forests under various Sky Conditions

Sigrid Dengel [1,2] and John Grace [1,2]

[1] Institute of Atmospheric and Environmental Science, School of GeoSciences,
Crew Building, University of Edinburgh, EH9 3JN, UK
[2] NERC NCEO/Centre for Terrestrial Carbon Dynamics, Sheffield, UK

# 3. $CO_2$ exchange and canopy conductance of coniferous forests under various sky conditions

## 3.1. Abstract

Sky conditions play an important role in the Earth's climate system and carbon dioxide ($CO_2$) uptake by plants. It is well known that the $CO_2$ uptake by forests is enhanced under diffuse skylight.

We chose several days of eddy covariance (EC) and meteorological data, including global and diffuse photosynthetic active radiation (PAR), recorded over the 2008 growing season at two Sitka spruce [*Picea sitchensis (Bong.) Carr.*] forest sites in northern Britain, in order to establish relationships between diverse sky conditions, such as (i) sunny, (ii) cloudy and (iii) overcast and several canopy activity related properties. These properties are (a) light response, (b) photosynthetic light use efficiency (LUE) and (c) canopy stomatal conductance ($g_c$) of this spruce species. We found that Sitka spruce forests utilise PAR in a more efficient way when solar radiation is dominated by diffuse radiation. Furthermore, our results show a distinctive effect of diffuse radiation on canopy stomatal conductance and the dependency of photosynthesis on $g_c$.

Key words: diffuse radiation, canopy conductance, $CO_2$ exchange, light response, spruce.

## 3.2. Introduction

Water vapour ($H_2O$) and carbon dioxide ($CO_2$) play crucial roles in the climate system, and both are exchanged between vegetation and the atmosphere through stomata (Anderson *et al.,* 2000; Blanken & Black, 2004; Kumagai *et al.,* 2004), which constantly modify the resistance to gas exchange in response to changing environmental conditions to maintain plant growth while minimizing water loss (Beadle *et al.,* 1985; Jarvis & McNaughton, 1986; Leuning, 1995; Anderson *et al.,* 2000; Buckley, 2005).

The major role of stomata is to limit the exit of water vapour which evaporates from the cell walls in contact with air spaces within the leaf, whilst at the same time allowing entry of $CO_2$ for photosynthesis. The extent to which stomata conduct water vapour and carbon dioxide at the canopy scale (i.e. canopy conductance, $g_c$) depends on the amount of leaves and several environmental controls (Kaufmann, 1976; Blanken, 2002; Kumagai *et al.,* 2004).

An over-riding environmental factor influencing water loss, photosynthesis and canopy conductance is solar radiation (Kaufmann, 1976; Zeiger, 1983, 1990). However several authors have shown that gas exchange at canopy scale depends not only on the incident solar radiation but also on the sky conditions (Gu *et al.,* 1999; Roderick *et al.,* 2001; Gu *et al.,* 2002; Gu *et al.,* 2003; Letts *et al.,* 2005; Min, 2005; Urban *et al.,* 2007; Mercado *et al.,* 2009); in particular, under diffuse skylight the rate of photosynthesis is enhanced. On a global scale, this phenomenon is a matter of great significance in relation to the likely stimulation of plant productivity by aerosols, particularly anthropogenic pollution (Roderick *et al.,* 2001; Farquhar & Roderick, 2003; Mercado *et al.,* 2009). Diffuse light is thought to penetrate more deeply into the canopy, and may have spectral characteristics that elicit stomatal opening (Urban *et al.,* 2007).

Previous measurements (Dengel *et al.*, previous chapter) have shown that light quality (spectral distribution) and quantity (amount) measured under (i) sunny conditions (ii) Altostratus cloud cover and (iii) during overcast conditions differed substantially within the forest canopy. The blue (400-500 nm) and the red (600-700 nm) part of the photosynthetic active radiation (PAR - 400-700 nm) band are important wave bands and a much higher proportion of blue light was observed under diffuse sky conditions within the Sitka spruce canopy than under sunny conditions. Smith (1982) reports that the opening of stomata is controlled by both light quantity and light quality, while Morison & Jarvis (1983) demonstrated that blue wavelengths are more effective in causing stomatal opening than red wavelengths while the opposite is the case for net $CO_2$ assimilation. Similar findings were reported by Zeiger (1983), noting that an increase in far-red light increased photosynthesis without affecting stomatal conductance. Blue light has a positive effect on opening of stomata (Raschke, 1975), with blue light being up to 20% more effective in opening stomata than red light (Willmer, 1983; Karlsson, 1986; Eisinger *et al.*, 2000; Briggs & Christie, 2002).

At a larger scale, other factors influencing photosynthetic and stomatal characteristics of the foliage have been reported by Schaefer *et al.* (2000) as being tree height and by Jarvis (1987) as being social status of trees, position of the foliage in the vertical in the horizontal, branching hierarchy and age of leaves. All these factors may interact with the manner in which radiation penetrates the plant canopy, and are dependent on the management of the forest. Thinning, for example, will affect the distribution of light and hence alter rates of photosynthesis

In this chapter we report the carbon dioxide exchange characteristics of Sitka spruce plantations under different conditions of skylight i.e. direct and diffuse. We examine the hypothesis that the photosynthetic response is constrained by stomatal conductance which varies between conditions of direct versus diffuse radiation.

## 3.3. Sites and methods

### 3.3.1. Site characteristics

Half-hourly eddy covariance measurements (Priestley & Swinbank, 1947; Desjardins & Lemon, 1973; Bakan, 1978; Baldocchi *et al.*, 1988; Moncrieff *et al.*, 1997; Aubinet *et al.*, 2000; Baldocchi, 2003), including fluxes of $CO_2$ ($F_c$), $H_2O$ (latent heat - $\lambda E$) were measured following methods described in Moncrieff *et al.* (1997) and Aubinet *et al.* (2000) at two Sitka spruce [*Picea sitchensis (Bong.) Carr.*] forests. The sites were: Harwood (Northumberland, England) (Zerva *et al.*, 2005; Ball *et al.*, 2007) and Griffin (Perthshire, Scotland) (Clement *et al.*, 2003 and Clement, 2004), two managed plantations of similar age. The forests are very similar, except for the fact that Griffin has had a management intervention, 1 in 5 rows having been removed in 2004. The Harwood site is located in a plot planted in 1976 with a leaf area index (LAI) of 7, while Griffin is located in a plot planted on a 7° slope in 1982 and thinned in 2004 with a current LAI of around 5. Flux measurements in Harwood were done with a closed path system (Jarvis, 1995; Moncrieff *et al.*, 1997; Haslwanter *et al.*, 2009), while flux measurements in Griffin were done with an open path system (Haslwanter *et al.*, 2009). These measurements were accompanied by high resolution global ($Q_g$) and diffuse ($Q_d$) photosynthetic active radiation (PAR) measurements using a Delta-T BF3 (Delta-T Devices Ltd, Burwell, UK) (Wood *et al.*, 2003; Muneer *et al.*, 2007) sunshine sensor as well as temperature ($T_a$), relative humidity ($R_h$) (Campbell Scientific, Utah, USA), surface wetness ($S_w$) (Skye Instruments, Llandrindod, UK) and several other meteorological variables.

Data used in the current study were recorded over the 2008 growing season and divided into spring/bud break (May-June) and summer/growing (July-October) periods. Furthermore single days were chosen which show the same or similar radiation conditions as used for the previous experiment (Dengel *et al.*, previous chapter) in order to investigate light response and canopy conductance at these two spruce forest locations. In order to reproduce possible cloud cover types, we followed methods found in Falconer (1965); Duchon & O'Malley (1999) and Calbo *et al.* (2001). These were sunny days where the diffuse fraction was lower than 0.3 (Urban *et al.*, 2007), days with diffuse fraction > 0.3, as well as overcast days where diffuse fraction was > 0.95.

### 3.3.2. Flux measurements

The eddy covariance (EC) setup in Harwood includes a closed path system, described in Jarvis (1995) and Moncrieff *et al.* (1997), which includes the fast response (20Hz) Li-6262 infra red gas analyser (IRGA) (LI-COR, Lincoln, NE, USA) which measures carbon dioxide ($CO_2$) and water vapour ($H_2O$) fluxes. This setup uses nitrogen ($N_2$) as a $CO_2/H_2O$ free reference gas and requires a continuous flow of a reference gas through the reference cell. The ultrasonic anemometer used in this setup is manufactured by Gill (Solent R3, Gill Instruments, Lymington, UK). Sample air is drawn through a Dekabon™ tube (Megaflex Ltd, Southwell, UK) and through the gas analyser by a diaphragm pump. The eddy covariance data were acquired with EdiSol, the software developed and written at the University of Edinburgh (Moncrieff *et al.,* 1997; Clement, 2004) and originally derived from EddySol (Jarvis, 1995). EdiSol calculates real-time fluxes of carbon and water vapour, as well as sensible and latent heat, along with momentum and displays them in a user friendly way on a common Laptop PC as part of the logging system.

### 3.3.3. Light response and photosynthetic capacity

Ecosystem respiration ($R_e$) was calculated for each half-hour from site-specific relationships between nocturnal net ecosystem exchange (NEP) and air temperature following Goulden *et al.* (1997); Law *et al.* (2002) and Nichol *et al.* (2002).

Windy (u* > 0.2 m $s^{-1}$) night time flux data were plotted against air temperature ($T_a$) measured on top of the eddy flux towers and the exponential function of

$$R_e = a\mathrm{e}^{bTa} \tag{1}$$

fitted, where $R_e$ is respiration, $a$ and $b$ are constants and $T_a$ air temperature. e is the base of the natural logarithm. Daytime respiration was calculated from this function using daytime air temperature. GEP was calculated by removing the temperature corrected respiration from NEP.

Many authors (Watts *et al.*, 1976; Jarvis, 1987; Causton & Dale, 1990; Jarvis, 1994; Raupach, 1995; Ruimy *et al.*, 1995) assume a rectangular hyperbola relationship between canopy photosynthesis and photosynthetic active radiation (PAR) where the rectangular hyperbola gradually approaches a maximum rate of photosynthesis, as PAR increases. The response is asymptotic, and the parameters depend on leaf photosynthetic properties and environment.

$$F_{CO_2} = \frac{A_{\max} Q_g}{\left(b + Q_g\right)} \tag{2}$$

with $F_{CO_2}$ describing the photosynthetic light response, $Q_g$ incident global PAR (µmol $m^2$ $s^{-1}$), $A_{max}$ the maximum gross photosynthesis at infinite irradiance and $b$ is the PAR value at which half of the photosynthetic saturation is occurring. In our case equation (2) describes gross photosynthesis, and so the curve passes through the origin. $A_{max}/b$ is the gradient of the curve at $A_{max}$ = 0, representing the photochemical efficiency (LUE) (Causton & Dale, 1990). This calculation was done for the entire season with selected days grouped into the three scenarios mentioned above. 2008 was a very wet growing season where sunny days were very rare.

Only one sunny day per growing period could be used for Harwood in the current investigation. For cloudy and overcast analysis 3 or more days were used. All days used for analysis were completely dry days.

### 3.3.4. Canopy conductance and photosynthetic capacity

Canopy conductance ($g_c$) was determined for the same groups of days. These were (i) sunny days where the diffuse fraction was lower than 0.3 (Urban *et al.,* 2007), (ii) bright cloudy days with very high global and higher diffuse fraction (> 0.3) and (iii) overcast days where diffuse fraction was > 0.95.

Canopy conductance ($g_c$) was determined by rearranging the Penman-Monteith equation (e.g. Bernhofer *et al.,* 1996; Blanken & Black, 2004; Clement, 2004; Harris *et al.,* 2004; Kumagai *et al.,* 2004; Komatsu *et al.,* 2005; Urban *et al.,* 2007):

$$1/g_c = \left[\left(\frac{s}{\gamma}\right)\beta - 1\right]\left(1/g_a\right) + \frac{\rho_a c_p}{\gamma}\frac{D_a}{\lambda E} \quad \text{(Blanken \& Black, 2004),} \tag{3}$$

where in eqn. (3) $g_c$ is the canopy conductance, *s* the rate of the increase of saturation vapour pressure with air temperature, $\gamma$ the psychrometric constant, $\beta$ the Bowen ratio (ratio between sensible and latent heat), $g_a$ the aerodynamic conductance, $\rho_a$ density of dry air, $c_p$ the specific heat of air, $D_a$ saturation deficit and $\lambda E$ is the latent heat flux obtained from eddy covariance measurements.

Aerodynamic conductance was estimated according to Thom (1975); Granier *et al.* (2000); van der Tol *et al.* 2003 as follows:

$$g_a = \frac{\mathrm{k}^2\mathrm{u}}{\ln[(\mathrm{z}-\mathrm{d})/\mathrm{z}_0]}, \tag{4}$$

where *k* is the von Karman constant (0.41), *u* the wind speed measured at the height *z*. $z_0$ is the surface roughness (=0.1*h* where *h* is the mean canopy height) and *d* the zero plane displacement (=0.64*h*) (Cowan, 1969; Seginer, 1974) (eqn 4).

## 3.4. Results

### 3.4.1. Light response estimates - seasonal variability

Light response curves were estimated for both forest sites and separated by growing periods into spring (bud break season) and summer (growing season). Results are illustrated in Figure 3.1, representing Harwood forest in Fig. 3.1 (a & b) and Griffin forest in Fig. 3.1 (c & d). Data points were left out for clarity. There are distinctive similarities but also differences between the two sites. Light use efficiency estimates were derived as the initial slope of these curves and can be found in Table 3.1.

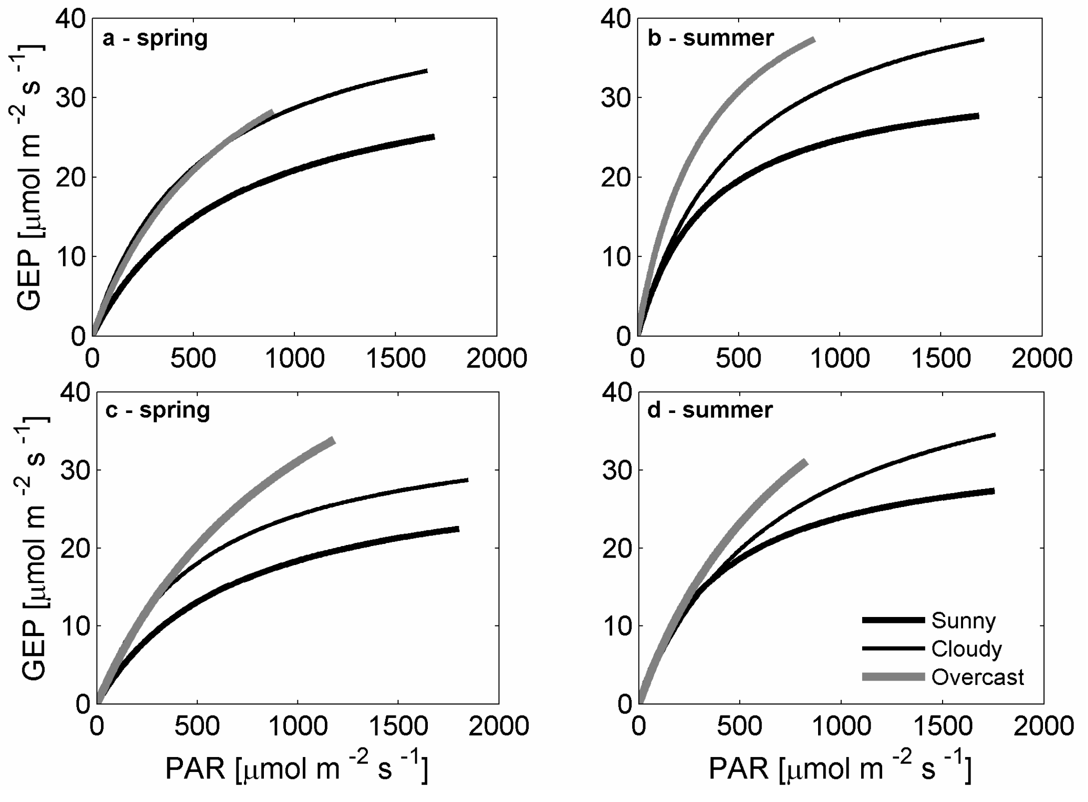


Figure 3.1: Photosynthetic light response curves for Harwood (a & b) and Griffin Forest (c & d).
Data have been separated into three sky types i.e. sunny, cloudy and overcast. Due to bad weather conditions during the entire 2008 growing season only 1 sunny/clear day per growing period could be used for Harwood. 6 days each were used for cloudy conditions and 3 days each for overcast conditions in Harwood. 4 sunny days were used for spring analysis in Griffin and 3 for the summer period. 7 days each were used as cloudy days and 4 each for overcast conditions.

Parameters estimated from light response calculations are shown in Table 3.1. The initial slope is an estimation of the light use efficiency (LUE) or apparent quantum yield of the forest canopy (mol $CO_2$ per mol photons). A slope value of 0.05 indicates that in order to assimilate 0.05 mol $CO_2$ 1 mol of photons is necessary. This means 20 photons are required for the canopy to take up 1 mol $CO_2$. $A_{max}$ is the light-saturated rate of gross $CO_2$ assimilation (net rate of $CO_2$ assimilation and dark respiration) at infinitely high irradiance.

| Site | Sky condition | $A_{max}$ | B | Slope (LUE) | $R^2$ |
|---|---|---|---|---|---|
| Harwood - Spring | Sunny | 35.4 ± 2.9 | 697 | 0.05 ± 0.01 | 0.92 |
| | Cloudy | 44.3 ± 1.8 | 546 | 0.08 ± 0.03 | 0.88 |
| | Overcast | 51.5 ± 6.8 | 737 | 0.07 ± 0.04 | 0.86 |
| Harwood - Summer | Sunny | 33.6 ± 2.0 | 358 | 0.09 ± 0.02 | 0.89 |
| | Cloudy | 48.7 ± 2.6 | 525 | 0.09 ± 0.03 | 0.78 |
| | Overcast | 52.2 ± 3.33 | 349 | 0.15 ± 0.07 | 0.88 |
| Griffin - Spring | Sunny | 31.1 ± 1.7 | 697 | 0.04 ± 0.01 | 0.85 |
| | Cloudy | 36.7 ± 1.3 | 518 | 0.07 ± 0.02 | 0.85 |
| | Overcast | 66.4 ± 5.3 | 1137 | 0.06 ± 0.03 | 0.94 |
| Griffin - Summer | Sunny | 33.5 ± 1.3 | 400 | 0.08 ± 0.02 | 0.87 |
| | Cloudy | 48.9 ± 2.1 | 737 | 0.07 ± 0.03 | 0.87 |
| | Overcast | 65.6 ± 11.3 | 918 | 0.07 ± 0.04 | 0.82 |

Table 3.1: Parameters estimated from light response calculations. Data were separated into the same groups, as in Fig. 3.1. Table 3.1 is showing the estimated values for the maximum gross photosynthetic rate ($A_{max}$) with their according mean square error, the constant *b* as well as the here out estimated light use efficiency with their mean square error and $R^2$ the explained variance.

### 3.4.2. Variation in canopy conductance and photosynthetic capacity

In order to visualise the difference in canopy activity and meteorological properties, three representative and distinctive days for Harwood are summarized in Fig. 3.2: a sunny (diffuse fraction < 0.3) (Fig 3.2a - f), a cloudy (diffuse fraction > 0.3) (Fig 3.2g - l) and an overcast day (diffuse fraction > 0.95) (Fig 3.2m - r). Day time (defined as global radiation > 0 µmol $m^{-2}$ $s^{-1}$) values of $g_c$ have been plotted together with meteorological variables, such as global and diffuse radiation, along with air temperature ($T_a$), wind speed ($u$), net ecosystem productivity (NEP) measured on top of the eddy flux tower as well as the calculated vapour pressure deficit (VPD).

On days with a high direct radiation fraction canopy conductance is increasing steeply in the morning, but declines shortly before noon once global radiation is reaching values of higher than 1000 µmol $m^{-2}$ $s^{-1}$. The fraction of diffuse radiation remains stable at around 0.25 during the day. The environmental variables are strongly intercorrelated. Canopy stomatal activity and carbon fluxes show a similar pattern.

On overcast days where diffuse radiation is equal to global radiation, i.e. there is no direct illumination; the canopy conductance and NEP are almost as high as seen in the other two cases, despite the overall low PAR. Vapour pressure deficit (VPD) is somewhat lower, and this could explain some of the trends in $g_c$.

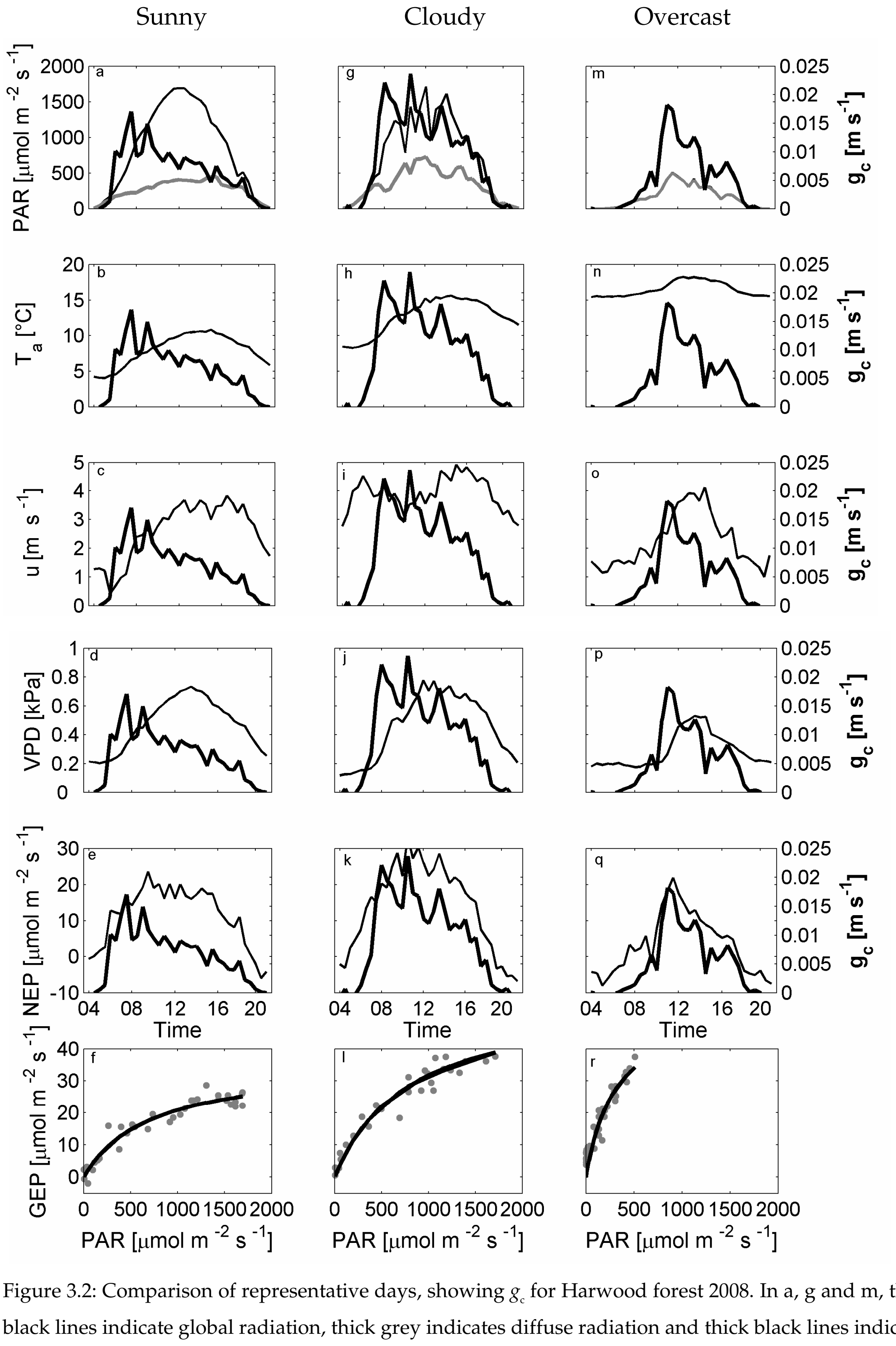


Figure 3.2: Comparison of representative days, showing $g_c$ for Harwood forest 2008. In a, g and m, thin black lines indicate global radiation, thick grey indicates diffuse radiation and thick black lines indicate $g_c$. The diurnal trend in $g_c$ is repeated in each window (except f, l and r) and superimposed on the diurnal trend of temperature ($T_a$), wind speed ($u$), VPD and NEP.

Canopy stomatal conductance calculated for Griffin forest show similar distributions on sunny days (Fig. 3.3), as already observed in Harwood forest. Carbon fluxes remain stable during the day reaching only values of 20 µmol $m^{-2}$ $s^{-1}$. On cloudy days with a less uniform direct radiation distribution and a diffuse fraction fluctuating between 0.25 and 0.75 stomatal conductance seems to remain constant, as wind speed does too. NEP on such a day indicates a higher carbon uptake when canopy conductance is approx 0.01 m $s^{-1}$. A similar effect is visible on the overcast day, where very high carbon uptake is occurring, though solar radiation is 100% diffuse and only 500 µmol $m^{-2}$ $s^{-1}$.

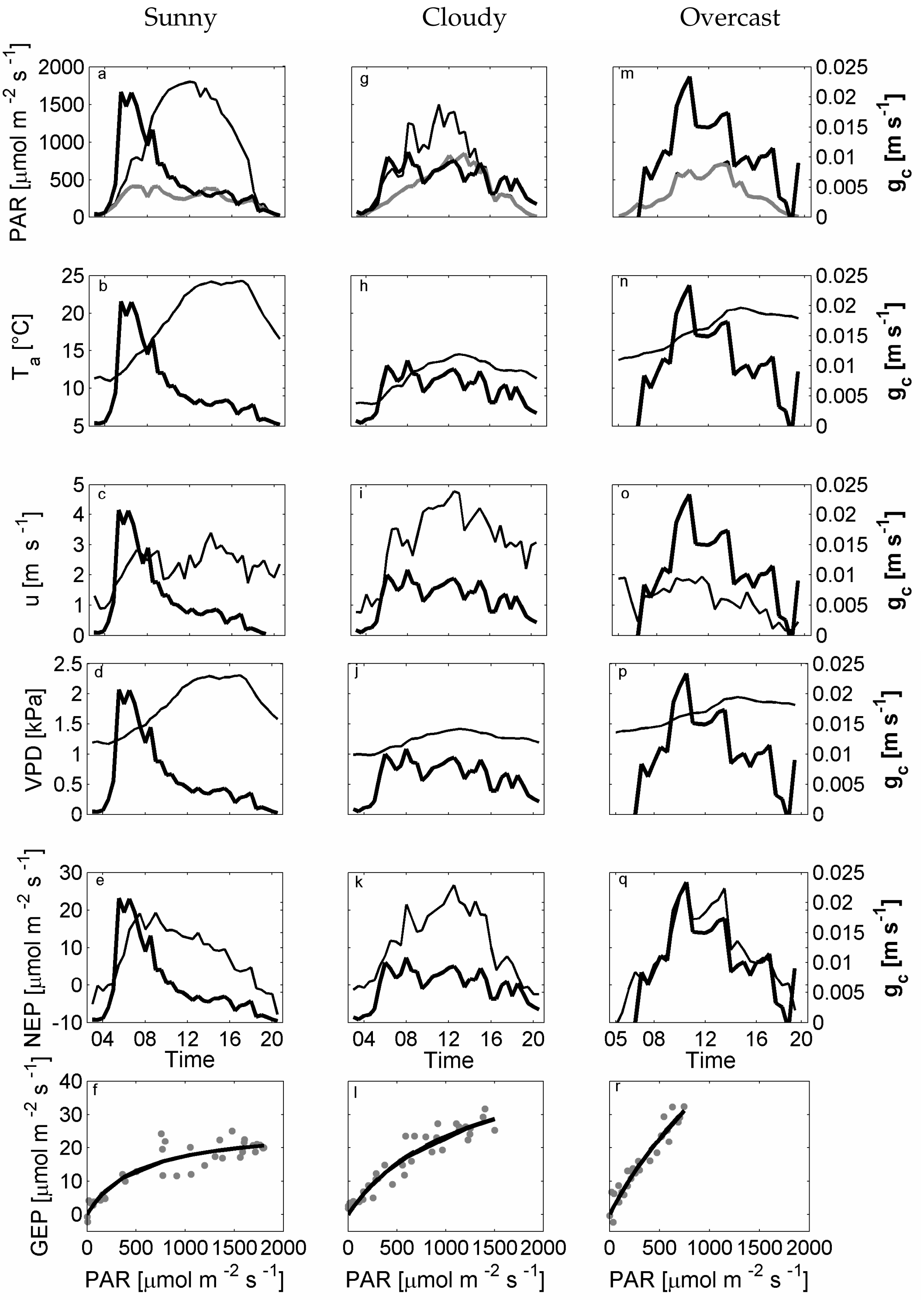


Figure 3.3: Comparison of representative days, showing $g_c$ for Griffin forest 2008. In a, g and m, thin black lines indicate global radiation, thick grey indicates diffuse radiation and thick black lines indicate $g_c$. The diurnal trend in $g_c$ is repeated in each window (except f, l and r) and superimposed on the diurnal trend of temperature ($T_a$), wind speed ($u$), VPD and NEP.

### 3.4.3. Canopy conductance

Fig. 3.4 (a & b) presents the canopy conductance dependency on global radiation for the same selected days as in Fig 3.2 and Fig 3.3. Harwood has a lower $g_c$ on sunny days compared to Griffin and same results for both forests on overcast days.

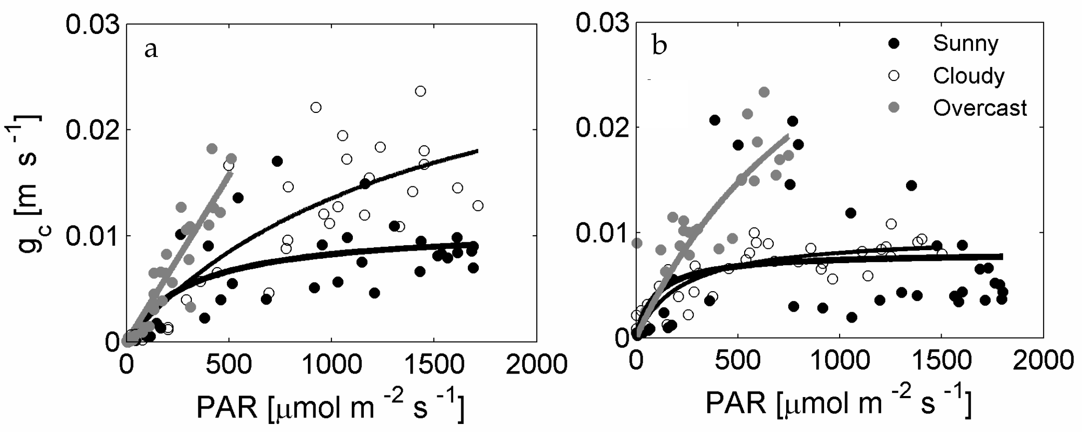


Figure 3.4: Relationship between canopy conductance ($g_c$) and photosynthetic active radiation (PAR) for Harwood (a) and Griffin (b). Data used for both graphs are of the presented days in Fig 3.2 (Harwood) and Fig 3.3 (Griffin). Thick black lines represent the relationship on the sunny, thin black line the cloudy and the thick grey line represents the relationship for the overcast day.

Incorporating all days chosen for the current investigation used for the entire growing season (May - October 2008) as also shown in Fig 3.1 we present the hyperbolic relationship between the incident global photosynthetic active radiation and canopy conductance for both sites in Fig 3.5 (a & b).

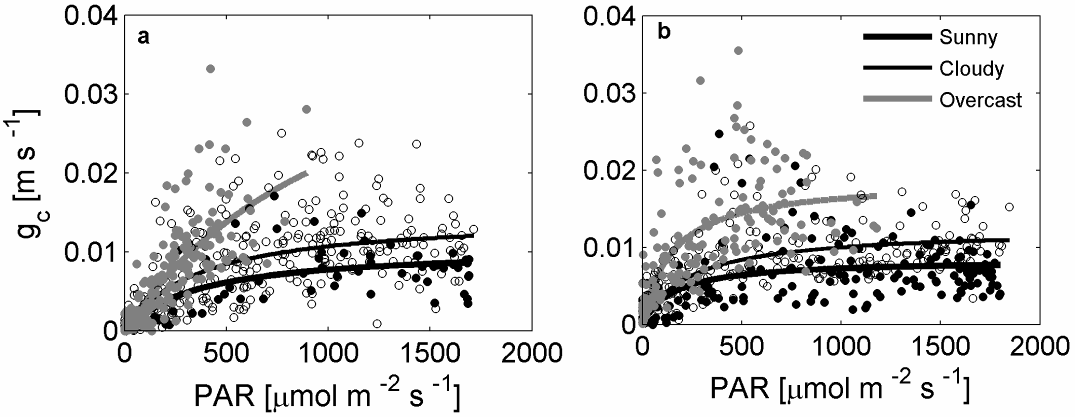


Figure 3.5: Relationship between canopy conductance ($g_c$) and photosynthetic active radiation (PAR) for Harwood (a) and Griffin (b) for all days of the entire growing season (May - Oct 2008). Data used for both graphs include all days as previously shown in Fig. 3.1. Due to bad weather conditions over the entire season 2008 sunny days in Harwood are represented by 2 days only. Black dots represent data on the sunny day, circles represent cloudy and grey dots represent overcast days**.**

The initial slope is much steeper under diffuse conditions (Fig. 3.5a & b) for both sites and sunny conditions elicit lowest $g_c$.

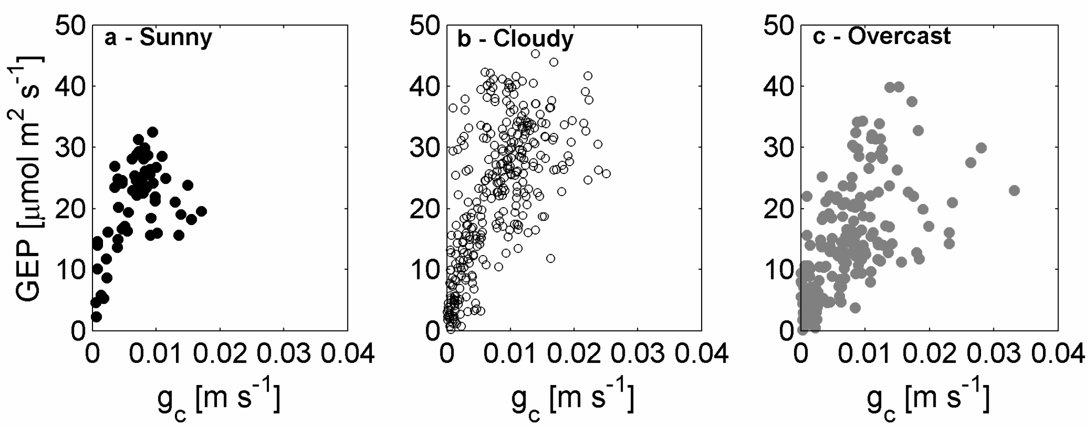


Figure 3.6: Harwood Forest. Distribution of canopy conductance ($g_c$) and gross ecosystem exchange (GEP) for all days of the entire growing season (May - Oct 2008). Data used include all days as previously shown in Fig. 3.1(a & b) and Fig 3.5(a). Due to bad weather conditions over the entire growing season 2008 sunny days are represented by 2 days only.

Fig 3.6 (a-c) shows the distribution of the stomatal canopy conductance and the gross photosynthesis in Harwood forest. The sunny data includes only 2 days and may underestimate the possibility of higher stomatal conductance and carbon assimilation on sunny days. Griffin data (Fig 3.7) incorporates several sunny days, supporting the Harwood result.

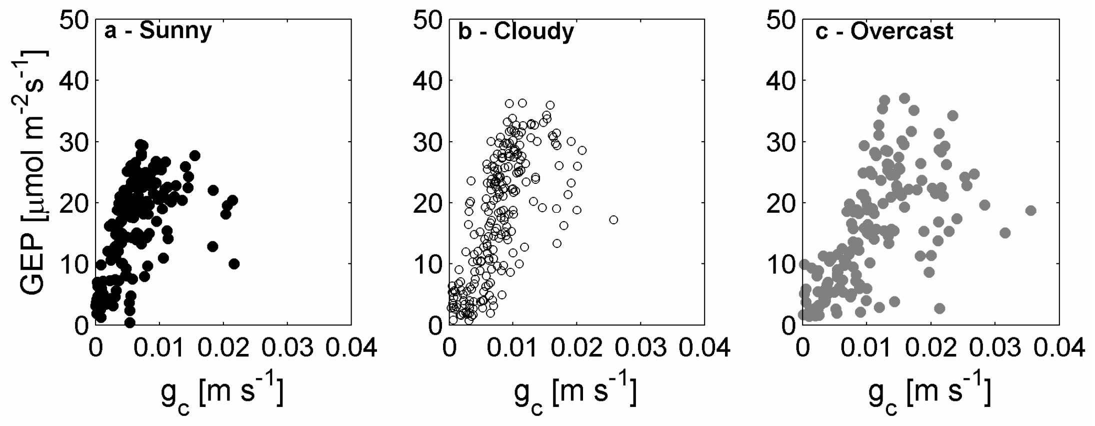


Figure 3.7: Griffin Forest. Distribution of canopy conductance ($g_c$) and gross ecosystem exchange (GEP) for all days of the entire growing season (May - Oct 2008). Data used include all days as previously shown in Fig. 3.1(c & d) and Fig 3.5(b).

The distribution of canopy stomatal conductance calculated for several days in Harwood (Fig. 3.6) and Griffin (Fig 3.7) and the associated gross photosynthesis show a distinctive pattern when comparing sunny versus cloudy or overcast conditions. Under sunny conditions, carbon assimilation never exceeds 30 μmol $m^2$ $s^{-1}$ and canopy conductance rarely exceeds 0.02 m $s^{-1}$. The relationship between $g_c$ and GEP under diffuse conditions appear similar but the higher $g_c$ allows higher photosynthetic responses.

### 3.5. Discussion and conclusion

We proposed the hypothesis that Sitka spruce is photosynthesising in a more efficient way under diffuse sky conditions than under clear skies. This hypothesis is supported by the fit of the rectangular hyperbola to the photosynthetic data under different sky conditions. In all cases the fitted values of $A_{\max}$ are less when conditions are sunny. In most cases the initial slope of the light response curve is lower in the sunny conditions indicating a reduced apparent quantum efficiency of the canopy. Other researchers have found similar results: Gu *et al.* (1999); Gu *et al.* (2002); Law *et al.* (2002); Letts *et al.* (2005); Min (2005); Alton *et al.* (2007); Urban *et al.* (2007) and as model outputs (Still *et al.,* 2009). These data refer to half-hourly averages. Over extended periods, the overall light use efficiency is expected to be greater in diffuse conditions although this is not necessarily so because the levels of PAR may be very low on overcast days in the cyclonic weather which is common in northern Britain.

A number of hypotheses have been put forward to explain why the initial slope of the light response curve may be enhanced in diffuse conditions (i) that PAR is more uniformly distributed within the canopy, so that more of the total foliage operates close to its leaf level maximum rate of photosynthesis; (ii) that the spectral properties of the PAR are more conducive to photosynthesis; and (iii) connected to (ii), that the stomata are more open as a result of the changed spectral properties under diffuse radiation.

These hypotheses are not mutually exclusive. However in this chapter we focus on hypothesis (iii). The basis for this are the observations, made several times (Kuiper, 1964; Mansfield & Meidner, 1966; Raschke, 1975; Sharkey & Raschke, 1981; Smith, 1982; Zeiger & Field, 1982; Morison & Jarvis, 1983; Karlsson, 1986; Eisinger *et al.,* 2000; Briggs & Christie, 2002 and Urban *et al.,* 2007) that blue light triggers stomatal opening.

In the previous chapter it was shown that above the canopy there was a slight enrichment of the blue under diffuse conditions but inside the canopy there was a large blue enrichment.

We explored the relationship between PAR and $g_c$, finding a very strong enhancement of $g_c$ under overcast, and to some extent under cloudy conditions.
In this case, we have chosen days in which there was no rain or dew, in order to obtain water flux data of relatively high quality. The only previous author to have reported a $g_c$ versus PAR relationship seems to be Urban *et al.* (2007) which was also for a species of spruce (*Picea abies*). Indeed, their results resemble ours. They found, however, that sunny conditions with high PAR (> 600 μmol $m^{-2}$ $s^{-1}$) impaired $g_c$, a feature they attributed to the high VPD which often accompanies sunny weather, which in their case reached 3.7 kPa. In our case VPD rarely exceeded 2 kPa. On the other hand we know that *Picea sitchensis* is very sensitive to VPD (Grace *et al.*, 1975; Neilson & Jarvis, 1975), with a $g_c$ response that is approximately linear.

However, we know that $g_c$ in this species is sensitive to blue light. Morison & Jarvis (1983) showed that blue light elicits stomatal opening in a range of 0 - 300 μmol $m^{-2}$ $s^{-1}$. In the present data we find that it is within this range, 0 - 300 μmol $m^{-2}$ $s^{-1}$, that the observed values of $g_c$ are much-elevated in diffuse conditions. Further clarification of whether blue light or reduced VPD causes the effect cannot made without experimental studies inside the canopy. VPD would need to be held constant in chambers, whilst blue light would have to be manipulated.

The controlling effect of $g_c$ on GEP is clearly suggested when the two variables are plotted against each other (Fig. 3.6 and 3.7). The two forests behave in much the same way. There is always a statistical relationship between $g_c$ and GEP, with rising $g_c$ associated with rising GEP. The $g_c$ values under overcast conditions show some higher values, and associated higher GEP. However, it is not possible to say how much of this effect is caused by blue light as opposed to a reduced VPD.

The diurnal patterns of $g_c$ reflect the influence of several environmental variables on stomatal conductance (Jarvis, 1976): the most influential variables are photon flux, temperature, water potential, vapour pressure and ambient $CO_2$ concentration. The variables are strongly intercorrelated, resulting in a rather characteristic pattern of $g_c$ over the course of each day. Both sites show similar results on sunny days with $g_c$ of around 0.02 m $s^{-1}$ and much higher values on more distinct diffuse and overcast days.

Monteith (1995) also observed a response of stomata to solar radiation as being stimulated as irradiance increases but also a tendency to close in response to a larger demand for water, as observed on sunny days in both forests. With a decrease in solar radiation and in VPD in the afternoon, stomata could continue to close or could partly reopen before finally closing towards sunset. Both sunny days (Fig 3.2a & Fig 3.3a) show similar canopy conductance pattern, which have also been observed by other studies. Watts *et al.* (1976) and Arain *et al.* (2002) observed identical stomatal conductance pattern on sunny days, with $g_c$ increasing in the morning until reaching a maxima around 10am. This mid-morning peak with a gradual decline thereafter may be a general phenomenon in forests (Shuttleworth, 1989; Zeiger, 1990). Many of the earlier data are based on leaf level measurements and the use of a null-balance diffusion porometer (Watts *et al.*, 1976). Using the same device Leverenz *et al.* (1982) measured stomatal conductances of approx 0.007 m $s^{-1}$. Also, Beadle *et al.* (1985) recorded similar $g_c$ of 0.005-0.007 m $s^{-1}$ in Scots pine. These leaf level type measurements are mirrored in behaviour and magnitude in current whole canopy conductance measurements.

Former eddy covariance studies in Griffin forest (Clement, 2004) over several growing seasons showed similar monthly mean values of $g_c$ as currently observed and also found that $g_c$ responded to radiation up to values of 300 - 400 W $m^{-2}$. Urban *et al.* (2007) noted a somewhat different behaviour in Norway spruce, where a *decrease* in $g_c$ was observed during sunny days at irradiance exceeding 1000 µmol $m^{-2}$ $s^{-1}$. A suggestion of a decrease is present in the current data (Fig.3.6a and Fig. 3.7a). This decline may result from the high VPD values around noon.

Studies in Douglas fir (Tan *et al.,* 1977; Leverenz, 1981) indicated a possible reopening of stomata in the afternoon, and show generally similar results as those currently observed in Harwood and Griffin forest.

This pattern of stomatal closure induced by high direct radiation and an increase in air temperature occurs in order to prevent excessive water loss (Alton *et al.*, 2007). Willmer (1983) reports that relatively low levels of light (less than 1% of full sunlight) stimulate stomatal opening in leaves and the level needed to saturate the opening response is usually well below full sunlight. In most species stomata on the abaxial (lower) leaf surface are more sensitive to light than the adaxial (upper) stomata: they open at lower light levels and have wider open stomata at all light levels than adaxial stomata (Pemadase, 1979; Willmer, 1983). Kaufmann (1976) found a stomatal response to humidity and temperature in Engelmann spruce suggesting that spruce stomata respond simultaneously to the effect of light on photosynthesis and to the effects of vapour pressure gradients from leaf to air. Fully open stomata provide no advantage in these conditions since $CO_2$ gain is low and water loss may be substantial.

On days where forest ecosystems experience high radiation distributions and a coupled increase in temperature and decrease in humidity, stomatal relationships with these variables become especially important. Several studies on Sitka spruce (Grace *et al.,* 1975; Neilson & Jarvis, 1975; Watts *et al.,* 1976, Watts & Neilson, 1978) show a relationship between these two and $g_c$ to some extent, which was not always visible in our whole canopy measurements. Grace *et al.* (1975) also found that a reduction in humidity causes stomata to partially close in order to avoid physiological drought and the possible development of a leaf water deficit. In Sitka spruce forests, where long term heat stress is rare due to the oceanic climate they grow in, diffuse radiation and VPD seem to be of higher importance than temperature or wind speed. Wind tunnel experiments (Grace *et al.,* 1975) with Sitka spruce seedlings show a weak relationship between stomatal conductance and wind speed. A small wind effect, may, therefore, be due to the sweeping away of the moist boundary layer at the high speeds, bringing drier ambient air into contact with the epidermis and the stomatal apparatus (Grace *et al.,* 1975; Dixon & Grace, 1984).

The canopy does not achieve its highest photosynthetic rates, nor its highest stomatal conductance when solar radiation is dominated by direct solar radiation. Stomatal closure leads to reduced $CO_2$ uptake and hence reduced growth rates (Landsberg, 2003). In overcast conditions, when solar radiation is 100% diffuse, blue light enrichment and low vapour pressure deficit may both contribute to an enhanced photosynthetic performance.

## 3.6. References

Alton PB, North PR, Los SO (2007) The impact of diffuse sunlight on canopy light-use efficiency, gross photosynthetic product and net ecosystem exchange in three forest biomes. *Global Change Biology* **13**, 776-787.

Anderson MC, Norman JM, Meyers TP, Diak GR (2000) An analytical model for estimating canopy transpiration and carbon assimilation fluxes based on canopy light-use efficiency. *Agricultural and Forest Meteorology* **101**, 265-289.

Arain MA, Black TA, Barr AG, Jarvis PG, Massheder JM, Verseghy DL, Nesic Z (2002) Effects of seasonal and interannual climate variability on net ecosystem productivity of boreal deciduous and conifer forests. *Canadian Journal of Forest Research* **32**, 878-891.

Aubinet M, Grelle A et al. (2000) Estimates of the annual net carbon and water exchange of forests: The EUROFLUX methodology. In *Advances in Ecological Research* **30**, 113-175.

Bakan S (1978) Note on the eddy correlation method for CO2 flux measurements. *Boundary-Layer Meteorology* **14**, 597-600.

Baldocchi DD (2003) Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biology* **9**, 479-492.

Baldocchi DD, Hicks BB, Meyers TP (1988) Measuring Biosphere-Atmosphere Exchanges of Biologically Related Gases with Micrometeorological Methods. *Ecology* **69**, 1331-1340.

Ball T, Smith K, Moncrieff JB (2007) Effect of stand age on greenhouse gas fluxes from a Sitka spruce [*Picea sitchensis (Bong.) Carr*.] chronosequence on a peaty gley soil. *Global Change Biology* **13**, 2128-2142.

Beadle CL, Neilson RE, Talbot H, Jarvis PG (1985) Stomatal Conductance and Photosynthesis in a Mature Scots Pine Forest .1. Diurnal, Seasonal and Spatial Variation in Shoots. *Journal of Applied Ecology* **22**, 557-571.

Bernhofer C, Blanford JH, Siegwolf R, Wedler M (1996) Applying single and two layer canopy models to derive conductances of a Scots pine plantation from micrometeorological measurements. *Theoretical and Applied Climatology* **53**, 95-104.

Blanken P (2002) Land/atmosphere interaction: canopy processes. In Encyclopedia of Atmospheric Sciences (ed. Holton JR, Curry JA, Pyle JA) Academic Press 1121-1130.

Blanken PD, Black TA (2004) The canopy conductance of a boreal aspen forest, Prince Albert National Park, Canada. *Hydrological Processes* **18**, 1561-1578.

Briggs WR, Christie JM (2002) Phototropins 1 and 2: versatile plant blue-light receptors. *Trends in Plant Science* **7**, 204-210.

Buckley TN (2005) The Control of Stomata by Water Balance. *New Phytologist* **168**, 275-291.

Calbo J, Gonzalez J-A, Pagegrave, SD (2001) A Method for Sky-Condition Classification from Ground-Based Solar Radiation Measurements. *Journal of Applied Meteorology* **40**, 2193-2199.

Causton DR, Dale MP (1990) The Monomolecular and Rectangular Hyperbola as Empirical-Models of the Response of Photosynthetic Rate to Photon Flux-Density, with Applications to 3 Veronica Species. *Annals of Botany* **65**, 389-394.

Clement R (2004) Mass and Energy Exchange of a Plantation Forest in Scotland Using Micrometeorological Methods. *PhD Thesis*. University of Edinburgh, pp 416.

Clement R, Moncrieff JB, Jarvis PG (2003) Net carbon productivity of Sitka Spruce forest in Scotland. *Scottish Forestry* **57**, 5-10.

Cowan IR (1968) Mass, heat and momentum exchange between stands of plants and their atmospheric environment. *Quarterly Journal of the Royal Meteorological Society* **94**, 523-544.

Desjardins RL, Lemon ER (1974) Limitations of an eddy-correlation technique for the determination of the carbon dioxide and sensible heat fluxes. *Boundary-Layer Meteorology* **5**, 475-488.

Dixon M, Grace J (1984) Effect of Wind on the Transpiration of Young Trees. *Annals of Botany* **53**, 811-819.

Duchon CE, O'Malley MS (1999) Estimating cloud type from pyranometer observations. *Journal of Applied Meteorology* **38**, 132-141.

Eisinger W, Swartz TE, Bogomolni RA, Taiz L (2000) The Ultraviolet Action Spectrum for Stomatal Opening in Broad Bean. *Plant Physiology* **122**, 99-106.

Falconer RE (1965) A Simple Method for Obtaining a Continupus Record of Presence and Type of Clouds in Sky During Day. *Pure and Applied Geophysics* **60**, 236-244.

Farquhar GD, Roderick ML (2003) Atmospheric science: Pinatubo, diffuse light, and the carbon cycle. *Science* **299**, 1997-1998.

Goulden ML, Daube BC, Fan SM, Sutton DJ, Bazzaz A, Munger JW, Wofsy SC (1997) Physiological responses of a black spruce forest to weather. *Journal of Geophysical Research-Atmospheres* **102**, 28987-28996.

Grace J, Malcolm DC, Bradbury IK (1975) The Effect of Wind and Humidity on Leaf Diffusive Resistance in Sitka Spruce Seedlings. *The Journal of Applied Ecology* **12**, 931-940.

Granier A, Biron P, Lemoine D (2000) Water balance, transpiration and canopy conductance in two beech stands. *Agricultural and Forest Meteorology* **100**, 291-308.

Gu L, Baldocchi DD, Wofsy SC, Munger JW, Michalsky JJ, Urbanski SP, Boden TA (2003) Response of a Deciduous Forest to the Mount Pinatubo Eruption: Enhanced Photosynthesis. *Science* **299**, 2035-2038.

Gu L, Baldocchi D, Verma SB, Black TA, Vesala T, Falge EM, Dowty PR (2002) Advantages of diffuse radiation for terrestrial ecosystem productivity. *Journal of geophysical Research* **107**, 4050.

Gu L, Fuentes JD, Shugart HH, Staebler RM, Black TA (1999) Responses of net ecosystem exchanges of carbon dioxide to changes in cloudiness: Results from two North American deciduous forests. *Journal of Geophysical Research* **104**, D24, 31,421-31,434.

Haslwanter A, Hammerle A, Wohlfahrt G (2009) Open-path vs. closed-path eddy covariance measurements of the net ecosystem carbon dioxide and water vapour exchange: A long-term perspective. *Agricultural and Forest Meteorology* **149**, 291-302.

Harris PP, Huntingford C, Cox PM, Gash JHC, Malhi Y (2004) Effect of soil moisture on canopy conductance of Amazonian rainforest. *Agricultural and Forest Meteorology* **122**, 215-227.

Jarvis PG (1976) The Interpretation of the Variations in Leaf Water Potential and Stomatal Conductance Found in Canopies in the Field. Philosophical Transactions of the Royal Society of London. Series B, *Biological Sciences* **273**, 593-610.

Jarvis PG (1987) Water and Carbon Fluxes in Ecosystems. Schulze, E.-D. and H. Zwoelfer (Ed.). *Ecological Studies Analysis and Synthesis* **61**. Potentials and Limitations of Ecosystem Analysis. 50-67.

Jarvis PG (1994) Capture of Carbon Dioxide by a Coniferous Forest. *Resource Capture by Crops*, 351-374.

Jarvis PG (1995) The role of temperate trees and forests in $CO_2$ fixation. *Plant Ecology* **121**, 157-174.

Jarvis P, Leverenz JW (1983) productivity of temperate, deciduous and evergreen forests. In Encyclopedia of Plant Physiology New Series, Vol. 12D, Physiological Plant Ecology IV Springer-Verlag Berlin, Heidelberg, 233-280.

Jarvis PG, McNaughton KG (1986) Stomatal Control of Transpiration - Scaling up from Leaf to Region. *Advances in Ecological Research* **15**, 1-49.

Karlsson PE (1986) Blue light regulation of stomata in wheat seedlings. II. Action spectrum and search for action dichroism. *Physiologia Plantarum* **66**, 207-210.

Kaufmann MR (1976) Stomatal Response of Engelmann Spruce to Humidity, Light, and Water Stress. *Plant Physiology* **57**, 898-901.

Komatsu H, Kumagai T, Hotta N (2005) Is surface conductance theoreticalty independent of reference height? *Hydrological Processes* **19**, 339-347.

Kuiper PJC (1964) Dependence upon Wavelength of Stomatal Movement in Epidermal Tissue of Senecio odoris. *Plant Physiology* **39**, 952-955.

Kumagai T, Saitoh TM, Sato Y, Morooka T, Manfroi OJ, Kuraji K, Suzuki M (2004) Transpiration, canopy conductance and the decoupling coefficient of a lowland mixed dipterocarp forest in Sarawak, Borneo: dry spell effects. *Journal of Hydrology* **287**, 237-251.

Landsberg J (2003) Physiology on forest models: history and the future. *Forest Biometry, Modelling and Information Sciences* 1, 49-63.

Law BE, Falge E, et al., (2002) Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agricultural and Forest Meteorology* **113**, 97-120.

Letts MG, Lafleur PM, Roulet NT (2005) On the relationship between cloudiness and net ecosystem carbon dioxide exchange in a peatland ecosystem. *Ecoscience* **12**, 53-59.

Leuning R (1995) A critical appraisal of a combined stomatal-photosynthesis model for $C_3$ plants. *Plant, Cell and Environment* **18**, 339-355.

Leverenz J (1981) Photosynthesis and transpiration in large forest-grown Douglas-fir: diurnal variation. *Canadian Journal of Botany* **59**, 349-356.

Leverenz J (1981) Photosynthesis and transpiration in large forest-grown Douglas-fir: diurnal variation. *Canadian Journal of Botany* **59**, 349-356.

Leverenz J, Deans JD, Ford ED, Jarvis PG, Milne R, Whitehead D (1982) Systematic Spatial Variation of Stomatal Conductance in a Sitka Spruce Plantation. *Journal of Applied Ecology* **19**, 835-851.

Mansfield TA, Meidner H (1966) Stomatal Opening in Light of Different Wavelengths: Effects of Blue Light Independent of Carbon Dioxide Concentration. *Journal of Experimental Botany* **17**, 510-521.

Mercado LM, Bellouin N, Sitch S, Boucher O, Huntingford C, Wild M, Cox PM (2009) Impact of changes in diffuse radiation on the global land carbon sink. *Nature* **458**, 1014-1017.

Min Q (2005) Impacts of aerosols and clouds on forest-atmosphere carbon exchange. *Journal of Geophysical Research* **110**.

Moncrieff JB, Massheder JM et al., (1997) A system to measure surface fluxes of momentum, sensible heat, water vapour and carbon dioxide. *Journal of Hydrology* **188-189**, 589-611.

Monteith JL (1995) Accommodation between transpiring vegetation and the convective boundary layer. *Journal of Hydrology* **166**, 251-263.

Morison JIL, Jarvis PG (1983) Direct and indirect effects of light on stomata. I. In Scots pine and Sitka spruce. *Plant, Cell and Environment* **6**, 95-101.

Muneer T, Kubie J, Wood J (2007) Evaluation of a new photodiode sensor for measuring global and diffuse irradiance, and sunshine duration. *ASME Journal of Solar Energy Engineering* **125** (1). 1-6.

Neilson RE, Jarvis PG (1975) Photosynthesis in Sitka Spruce (*Picea-Sitchensis (Bong) Carr*) .6. Response of Stomata to Temperature. *Journal of Applied Ecology* **12**, 879-891.

Nichol CJ, Lloyd J, Shibistova O, Arneth A, Roeser C, Knohl A, Matsubara S, Grace J (2002) Remote sensing of photosynthetic-light-use efficiency of a Siberian boreal forest. *Tellus* **B 54**, 677-687.

Pemadasa MA (1979) Movements of abaxial and adaxial stomata. *New Phytologist* **82**, 69-80.

Priestley CHB, Swinbank WC (1947) Vertical Transport of Heat by Turbulence in the Atmosphere. Proceedings of the Royal Society of London. Series A, *Mathematical and Physical Sciences* **189**, 543-561.

Raschke K (1975) Stomatal Action. Briggs, Winslow R. (Ed.). *Annual Review of Plant Physiology* **26**, 309-340.

Raupach MR (1995) Vegetation Atmosphere Interaction and Surface Conductance at Leaf, Canopy and Regional Scales. *Agricultural and Forest Meteorology* **73**, 151-179.

Roderick M, Farquhar G, Berry S, Noble I (2001) On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. *Oecologia* **129**, 21-30.

Ruimy A, Jarvis PG, Baldocchi DD, Saugier B (1995) CO 2 Fluxes over Plant Canopies and Solar Radiation: A Review. *Advances in Ecological Research* **26**, 1-53.

Schaefer KVR, Oren R, Tenhunen JD (2000) The effect of tree height on crown level stomatal conductance. *Plant Cell and Environment* **23**, 365-375.

Seginer I (1974) Aerodynamic roughness of vegetated surfaces. *Boundary-Layer Meteorology* **5**, 383-393.

Sharkey TD, Raschke K (1981) Effect of Light Quality on Stomatal Opening in Leaves of *Xanthium-Strumarium L. Plant Physiology* **68**, 1170-1174.

Shuttleworth W (1989) Micrometeorology of Temperate and Tropical Forest. *Micrometeorology of Temperate and Tropical Forest* **324**, 299-331.

Smith H (1982) Light Quality, Photoperception, and Plant Strategy. *Annual Review of Plant Physiology* **33**, 481-518.

Still CJ, Riley WJ, et al. (2009) Influence of clouds and diffuse radiation on ecosystem-atmosphere $CO_2$ and $CO^{18}O$ exchanges. *Journal of Geophysical Research* **114.**

Tan CS, Black TA, Nnyamah JU (1977) Characteristics of stomatal diffusion resistance in a Donglas fir forest exposed to soil water deficits. *Canadian Journal of Forest Research* **7**, 595-604.

Thom A (1975) Momentum, Mass and Heat Exchange of Plant Communities. In: J.L. Monteith (ed), *Vegetation and the Atmosphere* **1**, 57-110.

Urban O, Janous D, et al., (2007) Ecophysiological controls over the net ecosystem exchange of mountain spruce stand. Comparison of the response in direct vs. diffuse solar radiation. *Global Change Biology* **13**, 157-168.

van der Tol C, Gash JHC, Grant SJ, McNeil DD, Robinson M (2003) Average wet canopy evaporation for a Sitka spruce forest derived using eddy correlation-energy balance technique. *Journal of Hydrology* **276**, 12-19.

Watts WR, Neilson RE (1978) Photosynthesis in Sitka Spruce (Picea sitchensis (Bong.) Carr.). VIII. Measurements of Stomatal Conductance and $^{14}CO_2$ Uptake in Controlled Environments. *Journal of Applied Ecology* **15**, 245-255.

Watts WR, Neilson RE, Jarvis PG (1976) Photosynthesis in Sitka Spruce (*Picea sitchensis (Bong,) Carr.*): VII. Measurements of Stomatal Conductance and $^{14}CO_2$ Uptake in a Forest Canopy. *Journal of Applied Ecology* **13**, 623-638.

Willmer CM (1983) Stomata. Longman, London, New York, 166 pp.

Wood J, Muneer T, Kubie J (2003) Evaluation of a New Photodiode Sensor for Measuring Global and Diffuse Irradiance, and Sunshine Duration. *Journal of Solar Energy Engineering* **125**, 43-48.

Zeiger E (1983) The Biology of Stomatal Guard-Cells. *Annual Review of Plant Physiology and Plant Molecular Biology* **34**, 441-475.

Zeiger E (1990) Light perception in guard cells. *Plant, Cell and Environment* **13**, 739-744.

Zeiger E, Field C (1982) Photocontrol of the Functional Coupling between Photosynthesis and Stomatal Conductance in the Intact Leaf: Blue Light and Par-Dependent Photosystems in Guard Cells. *Plant Physiology* **70**, 370-375.

Zerva A, Ball T, Smith KA, Mencuccini M (2005) Soil carbon dynamics in a Sitka spruce (*Picea sitchensis (Bong.) Carr.*) chronosequence on a peaty gley. *Forest Ecology and Management* **205**, 227-240.

# Chapter 4

## Paper III: Relationships between Atmospheric Conditions and Tree Rings

Sigrid Dengel [1,2], Dominik Aeby[1] and John Grace [1,2]

[1] Institute of Atmospheric and Environmental Science, School of GeoSciences,
Crew Building, University of Edinburgh, EH9 3JN, UK
[2] NERC NCEO/Centre for Terrestrial Carbon Dynamics, Sheffield, UK

Paper prepared for submission to *New Phytologist*.

# 4. Relationships between Atmospheric Conditions and Tree Rings

## 4.1. Abstract

We investigated the interannual variation in the growth rings formed by Sitka spruce (*Picea sitchensis (Bong.) Carr.*) trees in northern Britain (latitude 55°) over the period 1961 – 2005, in an attempt to disentangle the influence of atmospheric variables acting at different times of year. Rather weak correlations between these variables and growth were found. However, there was a consistent and statistically significant relationship between growth of the trees and the flux density of cosmic radiation. Moreover, there was an underlying periodicity in growth, with four minima since 1961, resembling the period cycle of cosmic radiation. We discuss the hypotheses that might explain this correlation: the tendency of cosmic radiation to produce cloud condensation nuclei, which in turn increases the diffuse component of solar radiation, and thus increases the photosynthesis of the forest canopy.

Key words: Diffuse radiation, tree rings, cosmic rays, spruce, Britain, volcanic eruptions.

## 4.2. Introduction

It is important to understand how forests respond to climate change. Forests belong to the most extensive ecosystems on the planet and are a substantial part of the biosphere, which is one of four major pools, along with fossil carbon, the oceans, and the atmosphere, comprising the global carbon cycle (Schimel, 1995; Waring & Running, 1998; Byrne & Green, 2004; Grace, 2004). These climatic changes include those which are relatively well known such as temperature, but also those which are less well understood, including changes in cloud cover and atmospheric turbidity. Cloud and haze changes with the weather but also over long periods due to anthropogenic pollution as well as naturally occurring aerosols, such as pollen, dust or materials resulting from volcanic eruptions. By studying how atmospheric conditions, particularly diffuse radiation, affect forest growth, we might understand how forests respond to short-term changes in cloud cover and the much discussed longer-term phenomenon of 'global dimming' (Roderick *et al.,* 2001; Stanhill & Cohen 2001; Roderick, 2006) associated with industrial pollution.

Growth conditions change over years and decades, and the annual and periodic growth of needles, shoots and tree rings varies considerably (Spiecker, 1999). Active cell division in the vascular cambium layer produces cells which expand and displace the cambium in an outward direction. In trees from boreal and temperate latitudes, cambial activity is not constant throughout the year. This discontinuity causes the phenomenon of growth rings (Fritts, 1976; Creber, 1977; Schweingruber, 1988; Fritts, 1991). Yearly tree rings are added to the stem, recording the effect of the respective year's climatic conditions in which they grew. Dendrochronologists, seeking to reconstruct past climates, have often emphasized the role of temperature. In contrast, this study investigates the possible link of a wide range of climatological variables, including diffuse radiation over several decades.

Diffuse radiation is known to stimulate canopy photosynthesis primarily because it penetrates into the canopy more effectively than the direct solar beam (Suzaki *et al.*, 2003; Gu *et al.*, 2003; Urban *et al.*, 2007). There may also be an additional mechanism for this stimulation, associated with differences in the spectra of diffuse light versus direct sunlight (Federer & Tanner, 1966; Urban *et al.*, 2007). These shifts in spectral distribution of light do also, like temperature, affect stomatal conductance (Morison & Jarvis, 1983). We therefore expect annual growth rates to be significantly stimulated by diffuse light especially when received at high intensity, as during the spring and summer.

## 4.3. Materials and Methods

To examine the effects of diffuse radiation on growth, it is necessary to investigate long term tree growth patterns against a background of the interannual variability that reflects inherent seasonal variability of weather conditions over the years. In order to define this annual variability, meteorological data and tree ring information from nearby sites are used. Both Eskdalemuir and Ae, in the northern region of the Unided Kingdom, are under maritime influences. Being not only remote and free from major anthropogenic pollution Eskdalemuir has the longest diffuse radiation records in the UK (Aeby, 2007).

Discs from stems of Sitka spruce [*Picea sitchensis (Bong.) Carr.*] were available from the Forest of Ae (Dumfrieshire) (55°16′ N; 3°10′ W, 245 m asl). Although Eskdalemuir (Eskdalemuir Observatory 55°12′ N; 3°35′ W, 350 m asl.) and Ae are 25 km apart, both are remote sites far from local pollution and subject to the same changing weather patterns influenced by westerly and south westerly airflows, and large scale influences of atmospheric aerosol loading in the northern hemisphere. They are located in one of the wettest and most maritime regions of the UK, where drought is rare and summer temperatures do not fluctuate much from year to year.

The standardized methodology in tree ring research has been developed by dendrochronologists mainly for the reconstruction of summer temperatures (Schove, 1954; Spiecker, 1995; Briffa *et al.,* 1998; Kalela-Brundin, 1999; Gervais & MacDonald, 2001; Briffa *et al.*, 2002) or precipitation (Spiecker, 1995) over the past centuries.

To investigate the interannual variability in tree growth, discs from Sitka spruce sections of mature stems (below 1 m) were used. Thirty discs were provided by Forest Research, the research agency of the Forestry Commission, from Forest of Ae (Scotland).

The trees had been planted in 1953 and felled in February 2006 (the last growth ring being therefore 2005) following felling protocols laid out by Forest Research (Mochan & Gardiner, 2007). Prior to felling, North and West directions were marked on the bark, and the discs were frozen as soon as they were returned to the Forest Research station.

Discs were scanned on an A3 scanner and rings were counted in their frozen state using WinDendro (Version 2003a/b, Regent Instruments Inc., Quebec, Canada). This method enables an accurate measurement of the actual width, often ignored when using dried discs or tree cores which tend to shrink and crack during the drying process and may be differently affected by moisture content. None of the discs used in the final analysis showed anomalous growth patterns, such as branch development, injury marks or false rings which might have influenced the growth of the tree on its northern side. The north radius was measured, in order to avoid 'noise' caused by compression wood (east) or downwards slope extension compensation (west) wood. The southern radius was ignored as it may have been influenced by microclimatological variation caused by direct solar irradiance.

Tree rings increase over the first few years of growth and then decrease steadily towards the bark (Dinwoodie, 1962; Phipps, 1982), assuming no thinning or fertilization has interrupted the natural growth. This standard age trend was factored out by de-trending prior to analysis. This was done by (i) first removing data covering the first few years (the juvenile section) (ii) fitting a simple cubic spline to the remaining 45 ring width values. The residuals were taken as representing the effect of climate signals on tree growth (henceforth called the Growth Index).

Meteorological data at Eskdalemuir Observatory (Anonymous, 1909) including direct and diffuse solar radiation have been recorded by the British MetOffice (UKMO), and were provided by the British Atmospheric Data Centre (BADC). Where necessary, gaps were filled by two different methods. Either (i) a simple linear interpolation was applied or (ii) in the case of missing global or diffuse radiation data the data were replaced by a weighted mean of the same day of the neighbouring year (Aeby, 2007).

Cosmic ray fluxes are known to be dependent on latitude (Svensmark & Friis-Christensen, 1997; Pallé & Butler, 2000; Pallé et al., 2004; Kirkby, 2007). Monthly corrected galactic cosmic ray flux data recorded at Kiel Neutron Monitor are held by the Christian-Albrechts-Universitaet zu Kiel and information on the locality and time of volcanic eruptions, as well as on the Volcanic Explosivity Index relevant for this study originate from the Smithsonian Institution, Global Volcanism Program.

Our correlations are based on Pearson product-moment correlation coefficients between the growth index and the climatic and atmospheric factors of each month of the corresponding year and the previous year. The previous year is used because it is well known that in coniferous trees some aspects of growth in any given year are determined by the conditions prevailing in the previous year.

The numerical experiment introduced here is based on empirical curve-fitting of the relationship between the carbon dioxide ($CO_2$) flux measured by eddy covariance and the global solar radiation at a mature stand of Sitka spruce (Griffin forest, Aberfeldy/Scotland). Two curves were fitted: 'sun visible' and 'sun not visible'. Under 'sun not visible' conditions the initial slope of the relationship between solar radiation and $CO_2$ flux is steeper, as many other researchers have found (Farquhar & Roderick, 2003). The parameters of the non-rectangular hyperbolas used for the fitting are given in Zhang (2007).

## 4.4. Results

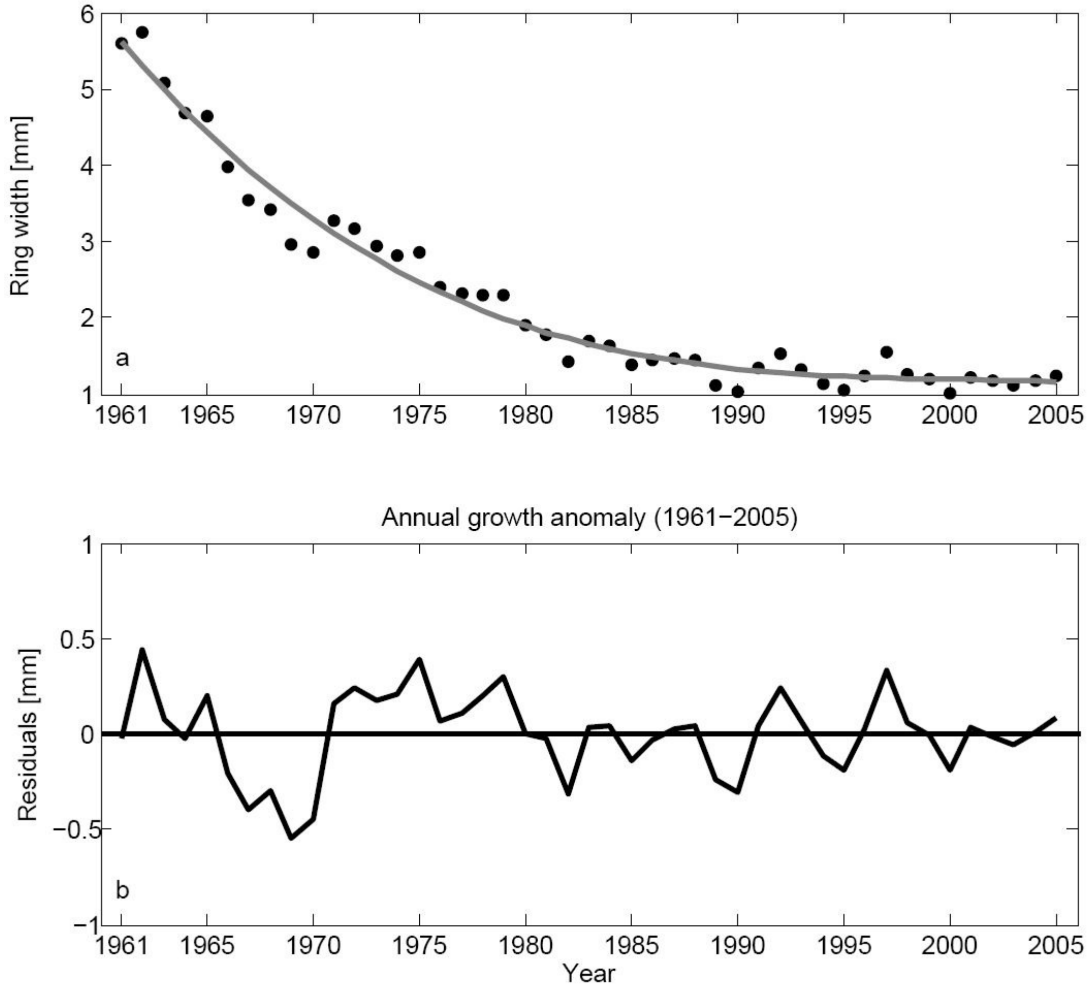


Figure 4.1: Distribution of the mean tree ring width (a) and the resulting annual growth anomaly (b) after applying the de-trending method.

The cubic spline represented the age-related decline in ring width very well ($r^2$ = 0.97), showing a characteristic decline in radial growth as the trees aged. The residuals suggest distinct periods of anomalous growth, and sometimes specific years when growth departed from the average trend.

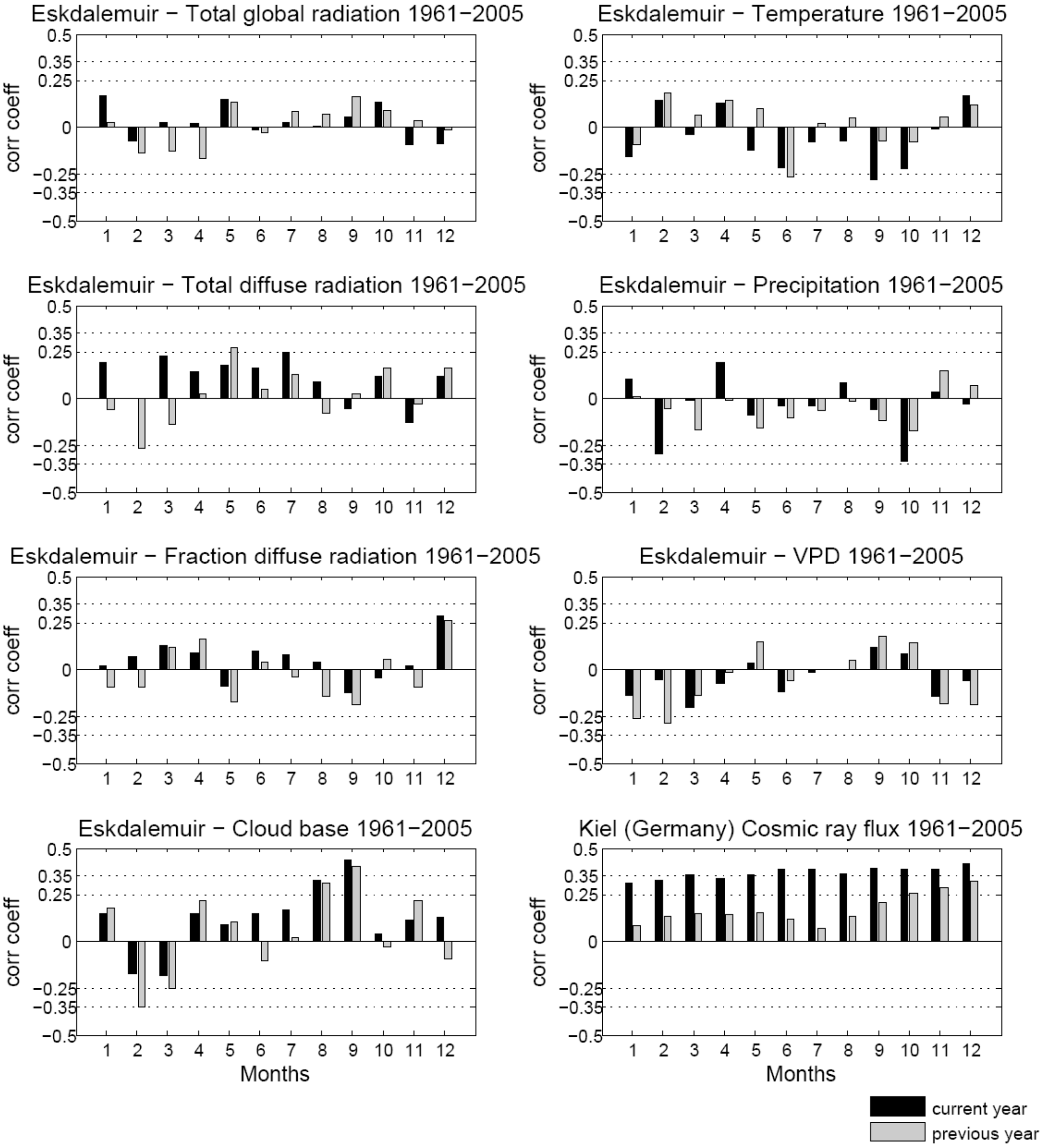


Figure 4.2: Pearson correlation coefficients between climatic variables recorded in Eskdalemuir (Scotland) between 1961 and 2005, and the growth index. The histograms show the correlations for the respective and the previous year. Correlation coefficient values of 0.25 and 0.35 respectively correspond to the ± 0.1 and ± 0.02 significance level.

Most variables were only weakly correlated with the annual growth anomaly: total solar radiation was never statistically significantly correlated with the annual growth anomaly but diffuse radiation was significantly correlated in some months (Fig. 4.2).

Temperature was negatively correlated with growth in the months of June and September, and precipitation was negatively correlated with growth in February and October. There were correlations between the annual growth anomaly and both the water vapour pressure deficit (VPD) and the calculated height of the most frequently occurring cloud base.

The cosmic ray flux shows a well known periodicity that is anticorrelated with the sunspot number with four maxima in the period 1961 – 2005 (Fig 4.3). Surprisingly, the tree ring data show a similar periodicity although it is possible to identify particular years where the relationship is broken: for example 1995 was an especially warm and dry year at Eskdalemuir as in much of Europe, and under these conditions the tree rings were reduced in size. The probability of such a good relationship between the growth index and cosmic ray flux occurring by chance alone is 0.008 (n = 45, r = 0.39) (see the inset of Fig. 4.3) of all the variables investigated, it is the one most correlated with the annual growth anomaly.

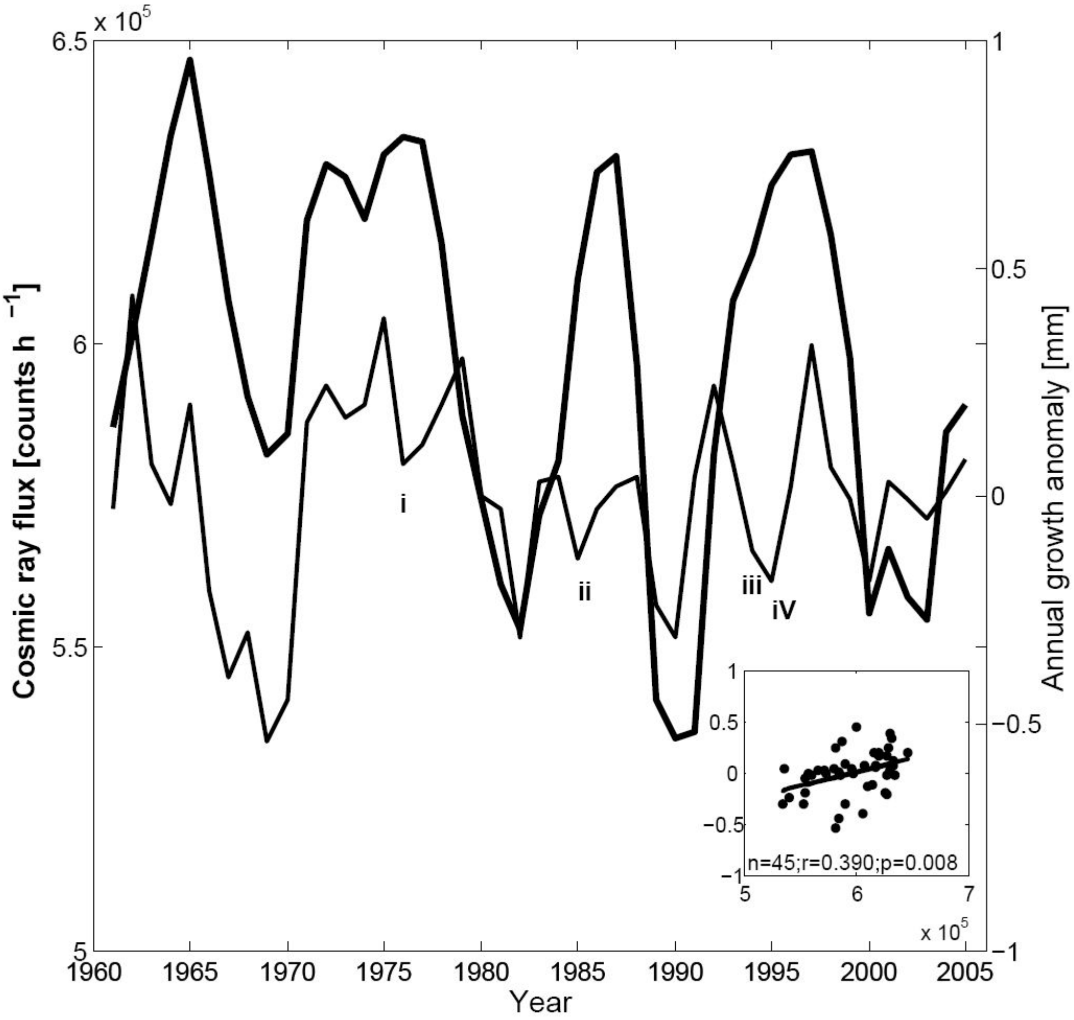


Figure 4.3: Cosmic ray flux (bold line) and the growth anomaly (thin line) of Sitka spruce. A distinct periodicity is visible with four distinctive maxima over the period 1961 – 2005. The inserted (lower right) graph shows the correlation (n=45, r=0.39, p=0.008) between the galactic cosmic ray flux and the annual growth anomaly. Instances of extreme weather are noted as follows: (i) in 1976 most parts of the UK experienced severe drought (Morren, 1980; Jarvis & Mullins, 1987; Kay, 2004), (ii) Eskdalemuir recorded snow in June 1985 (Burt, 1985), (iii) extreme cold and wet weather occurred in 1994 (UKMO, 2008a, 2008b) and (iv) 1995 was an especially warm and dry year in Scotland (Buckland *et al.*, 1997; UKMO, 2003) as in much of Europe. If anomalous years are excluded the correlation coefficient increases from 0.39 to 0.64 ($r^2 = 0.41$).

When the fraction of the incoming solar radiation which is received as diffuse radiation is examined in relation to the occurrence of volcanic eruptions with a Volcanic Explosivity Index (VEI) of 3 and higher which have erupted upwind (to the west of the UK) it appears that the fraction of diffuse radiation is often less in periods where there are few volcanoes (Fig 4.4).

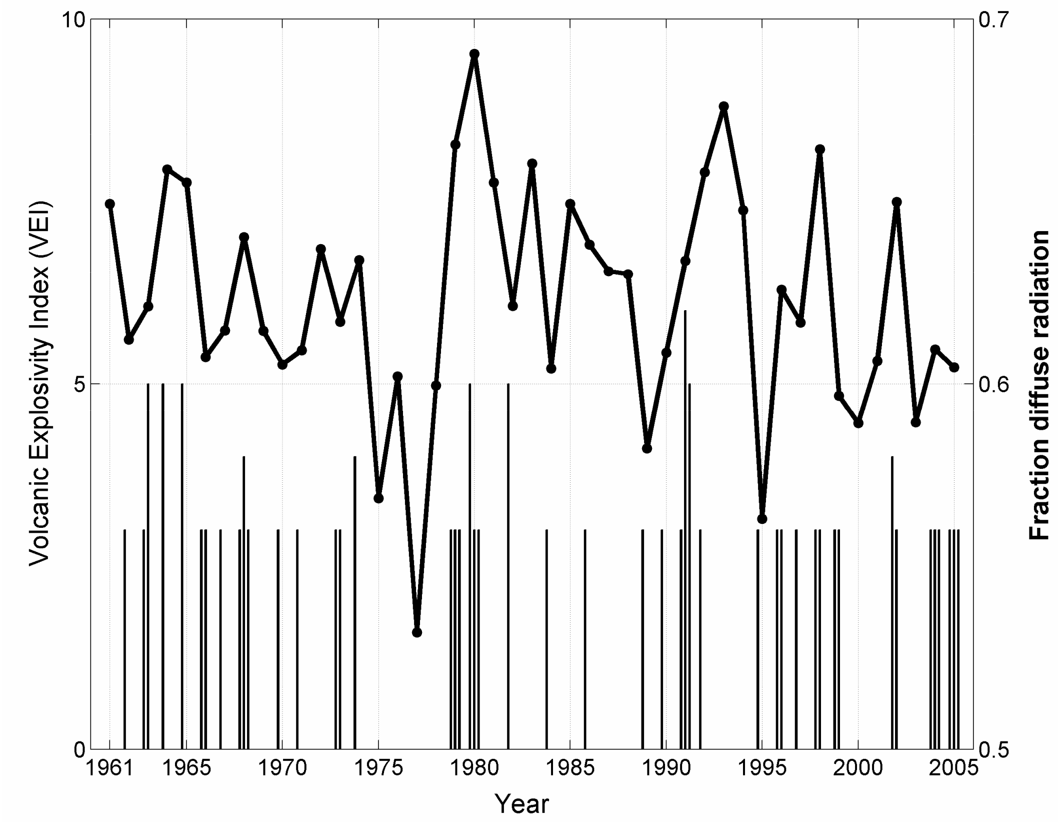


Figure 4.4: The fraction of diffuse radiation received at Eskdalemuir (Scotland) over the period 1961 – 2005 and volcanoes erupted upwind with an explosivity index of ≥ 3 (tephra volume >0.01 km$^3$). The volcanic explosivity index is a logarithmic scale indicating the magnitude and intensity (volume of produced ash, height of eruption cloud and the duration) of eruption.

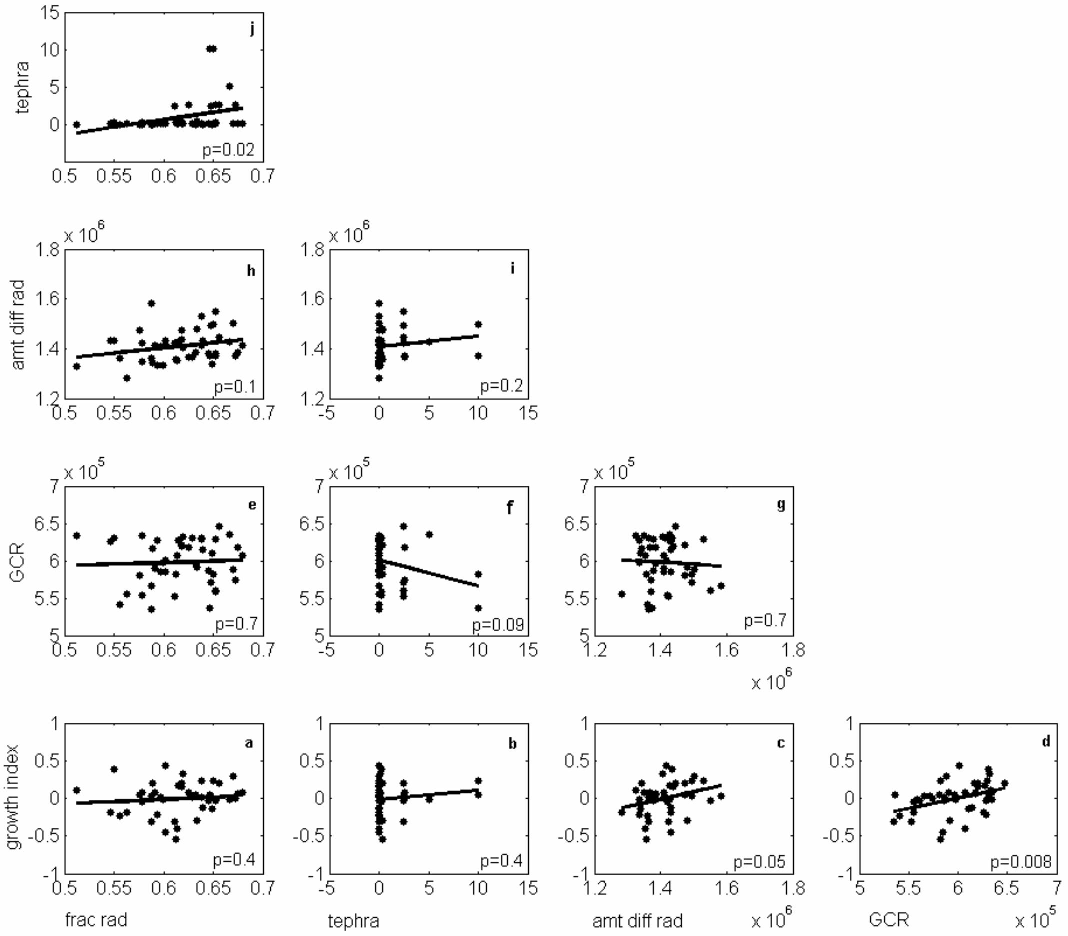


Figure 4.5: Correlation matrix including the growth index (annual growth anomaly) and the relevant variables used in previous figures. The lowest panel including Fig. 4.5a – d includes those atmospheric variables significant for tree growth, such as: (a) the fraction of diffuse radiation (spring + summer); (b) the mean potential tephra; (c) the amount of diffuse radiation (spring + summer) and (d) the galactic cosmic ray flux. When intercorrelating the atmospheric variables with each other, only the link between the mean potential tephra injected into the atmosphere and the fraction of the radiation received as diffuse seem to be highly correlated (j). Summarising here the remaining correlations: (e) the galactic cosmic ray flux vs. the fraction of diffuse radiation (spring + summer); (f) the galactic cosmic ray flux vs. the mean potential tephra; (g) the galactic cosmic ray flux vs. the amount of diffuse radiation (spring + summer); (h) the amount of diffuse radiation (spring + summer) vs. the fraction of diffuse radiation (spring + summer); (i) the amount of diffuse radiation (spring + summer) vs. the mean potential tephra and (j) the mean potential tephra vs. the fraction of diffuse radiation (spring + summer).

The correlation matrix (Fig. 4.5) shows a graphical summary of the relationship between the variables discussed above. This matrix is only part of a larger matrix in which many other tests of correlations were made. The variables influencing tree growth can be found in the lowest panel (Fig. 4.5a – d). When considering the diffuse radiation received over the spring and summer months (Fig. 4.5c), we observe a statistically significant correlation: the amount of diffuse radiation received over the March – August period is statistically positively correlated with the growth index, with a correlation coefficient of +0.29 ($p = 0.05$; $n = 45$). Fig. 4.5j tests for a relationship between the fraction of radiation that is diffuse and the likely content of volcanic-derived aerosols.

We have other evidence that growth may respond to diffuse radiation: when the diffuse component of global radiation is increased or decreased by 10% in a numerical experiment, the $CO_2$ uptake is increased by 11.7% or decreased by 25.6 % respectively (Fig. 4.6).

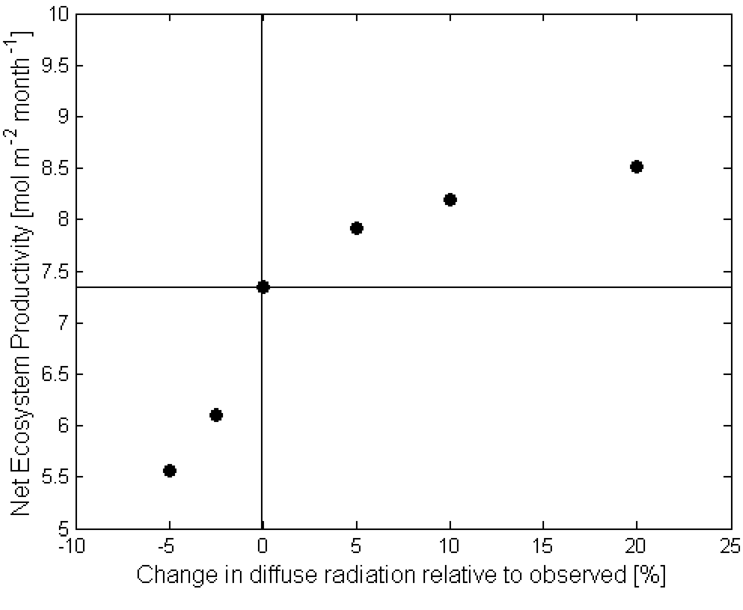


Figure 4.6: A numerical experiment involving the fraction of diffuse radiation and estimated NEP. A numerical experiment in which the fraction of diffuse radiation received in July was varied from -10% to +25%, and the Net Ecosystem Productivity (NEP) was estimated from real $CO_2$ flux data for a nearby forest of Sitka spruce (Zhang, 2007).

## 4.5. Discussion

There were correlations between annual growth anomaly and both the water vapour pressure deficit (VPD) and the height of the most frequently occurring cloud base. VPD has long been known to influence photosynthesis for the reason that the stomata close when the air is dry, especially in this species (Grace *et al.,* 1975; Neilson & Jarvis, 1975). Cloudiness *per se* may be expected to reduce plant growth through a reduction in solar insolation, although Williams *et al.,* (2008) have found that the effect of cloud cover on tree growth, and thus ring width, may vary depending on the type of cloud, the time of day, and the time of year.

We were surprised to see that the cosmic ray flux (Kiel Neutron Monitor, 54°34′ N; 10°12′ E, 54 m asl.) was statistically significantly correlated with the growth index in all months, and the first presumption is that cosmic rays create aerosols and thus change the radiation field. However, processes other than cosmic ray flux are involved in aerosol production and may also modify the radiation field, and thus mask any effect of cosmic radiation. Volcanic eruptions affect the flux of diffuse radiation received at the Earth's surface even when they are many thousands of miles away. While sulphur aerosols are capable of remaining in the atmosphere over 1 – 3 years and ashes only a few months, aerosols resulting from galactic cosmic rays have a much shorter lifespan. According to Yu & Turco, (2000); Kristjansson *et al.,* (2002) these aerosols have a lifespan of only a few days, so cloud formation and any consequent impact on photosynthesis should take place within this short time.

It has been observed that GCR cycles are correlated with cloud cover (Svensmark & Friis-Christensen, 1997; Marsh & Svensmark, 2000; Pallé & Butler, 2000a ; Pallé & Butler, 2000b) and that ionising radiation causes clouds to form in experimental chambers that simulate the Earth's atmosphere (Svensmark *et al.,* 2007). Moreover, a description of this process is presented by Yu & Turco (2000) and Harrison &

Carslaw (2003). Substantial ionising radiation is also produced from radioactive decay of elements below the surface of the soil (Kotaka & Kueger, 1978), and released to the atmosphere according to soil depth and moisture, but does not vary in cycles as we see in GCRs. The correlative studies linking GCRs to cloud formation have been challenged (Kristjansson *et al.*, 2002; Sun & Bradley, 2002; Laut, 2003), but the experimental studies (Svensmark et al. 2007) are compelling evidence for a role of cosmic rays in the process of cloud formation. Recent models (Kerr, 2009; Pierce & Adams, 2009) show only small effects of cosmic rays on clouds but are not denying the possibility of a link.

We propose the possible hypotheses to account for the strong link between galactic cosmic ray flux (GCR) and the annual growth anomaly. We call this hypothesis *the bright cloud effect*. To explain the link between GCRs and the growth index we propose that the forest 'sees' a radiation field that is to some extent modified by the aerosol particles derived from the flux of cosmic rays, but is not recordable with common solar radiation sensors.

We cannot however rule out the possibility of a direct stimulatory effect of GCR on the growth of trees, as beneficial effects have sometimes been demonstrated in biological materials exposed to GCR in space (Hammond *et al.*, 1996), despite the prevalence of chromosomal aberrations in such materials (Nevzgodina, 1999).

Dendrochronogists have sometimes reported cyclic phenomena in long time series of tree-rings but they have rarely offered an explanation (Douglass, 1927; Siren & Hari, 1971; Briffa, 1994; Rigozo *et al.,* 2007a, 2007b). For example, in a study of 305 tree-ring chronologies from North America, periods of 18.6 and 10.5 years were found in 286 and 244 instances (Currie, 1991). These observations have been largely ignored, perhaps because no underlying mechanism could be found to explain the intriguing results.

## 4.6. Acknowledgments

We thank Dr. Barry A. Gardiner and Dr. Mike Perks from Forest Research, Northern Station (Roslin, Scotland) for providing us with freshly cut tree discs used in the current study, for information on Forest of Ae and the initial help with the analysis of tree ring data with WinDendro. Furthermore, the authors would like to thank the British Atmospheric Data Centre (BADC) for the provision of meteorological data (UK Met Office) for Eskdalemuir.

Galactic cosmic ray flux data recorded at Kiel Neutron Monitor are held by the department of Extraterrestrial Physics, Institute for Experimental- and Applied Physics, Christian-Albrechts-Universitaet zu Kiel and provided by the National Geophysical Data Center, Boulder, Colorado (USA)
(ftp://ftp.ngdc.noaa.gov/STP/SOLAR_DATA/COSMIC_RAYS/kiel.tab - 31.05.2009). Information on the locality and time of volcanic eruptions, as well as on the Volcanic Explosivity Index relevant for this study originate from the Smithsonian Institution, Global Volcanism Program
(http://www.volcano.si.edu/world/find_eruptions.cfm - 31.05.2009).

## 4.7. References

Anonymous (1909) Eskdalemuir Observatory. *Nature* **81**, 86-86.

Aeby D (2007) Changes in Solar Irradiation at four Stations in the British Isles. *MSc Thesis*. The University of Edinburgh, 72 pp.

Briffa KR (1994) Grasping at shadows? A selective review of the search for sunspot-related variability in tree rings. *The Solar Engine and Its Influence on Terrestrial Atmosphere and Climate* **I 25**, 417–434.

Briffa KR, Osborn TJ, Schweingruber FH, Jones PD, Shiyatov SG, Vaganov EA (2002) Tree-ring width and density data around the Northern Hemisphere: Part 1, local and regional climate signals. *The Holocene* **12**, 737-757.

Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Shiyatov SG, Vaganov EA (1998) Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature* **391**, 678-682.

Buckland SM, Grime JP, Hodgson JG, Thompson K (1997) A Comparison of Plant Responses to the Extreme Drought of 1995 in Northern England. *Journal of Ecology* **85**, 875-882.

Burt, SD (1985) Sleet and snow in June 1985. *Weather* **40**, 222.

Byrne AK, Green C (2004) The role of forests in the global carbon cycle and in climate change policy. *Irish Forestry* **61**, 7 - 15.

Creber GT (1977) Tree Rings: A Natural Data-Storage System. *Biological Reviews* **52**, 349-381.

Currie RG (1991) Deterministic Signals in Tree-Rings from North-America.
*International Journal of Climatology* **11**, 861-876.

Dinwoodie JM (1962) Some Ring-width Pattern in Sitka Spruce Timber from North America. Foreststr 35, 22-26.

Douglass AE (1927) Solar Records in Tree Growth. *Science* **65**, 220-221.

Farquhar GD, Roderick ML (2003) Atmospheric science: Pinatubo, diffuse light, and the carbon cycle. *Science* **299**, 1997-1998.

Federer CA, Tanner CB (1966) Spectral Distribution of Light in Forest. *Ecology* **47**, 555-560.

Fritts HC (1976) Tree rings and climate. Academic Press: London New York, 567 pp.

Fritts HC (1991) Reconstructing large-scale climatic patterns from tree-ring data: a diagnostic analysis. University of Arizona Press, Tucson, 286 pp.

Gervais BR, MacDonald GM (2001) Tree-ring and summer-temperature response to volcanic aerosol forcing at the northern tree-line, Kola Peninsula, Russia. *The Holocene* **11**, 499-505.

Grace J (2004) Understanding and managing the global carbon cycle. *Journal of Ecology* **92**, 189-202.

Grace J, Malcolm DC, Bradbury IK (1975) The Effect of Wind and Humidity on Leaf Diffusive Resistance in Sitka Spruce Seedlings. *The Journal of Applied Ecology* **12**, 931-940.

Gu L, Baldocchi DD, Wofsy SC, Munger JW, Michalsky JJ, Urbanski SP, Boden TA (2003) Response of a Deciduous Forest to the Mount Pinatubo Eruption: Enhanced Photosynthesis. *Science* **299**, 2035-2038.

Hammond EC, Bridgers K, Berry FD (1996) Germination, growth rates, and electron microscope analysis of tomato seeds flown on the LDEF. *Radiation Measurements* **26**, 851-861.

Harrison RG, Carslaw KS (2003) Ion-aerosol-cloud processes in the lower atmosphere. *Reviews of Geophysics* **41**.

Jarvis NJ, Mullins CE (1987) Modeling the Effects of Drought on the Growth of Sitka Spruce in Scotland. *Forestry* **60**, 13-30.

Kalela-Brundin M (1999) Climatic information from tree-rings of Pinus sylvestris L. and a reconstruction of summer temperatures back to AD 1500 in Femundsmarka, eastern Norway, using partial least squares regression (PLS) analysis. *The Holocene* **9**, 59-77.

Kay J (2004) Dust to dust: The summer of 1976. *Weather* **59**, 247-250.

Kerr RA (2009) Study Challenges Cosmic Ray-Climate Link. *Science* **324**, 576-577.

Kirkby J (2007) Cosmic Rays and Climate. *Surveys in Geophysics* **28**, 333-375.

Kotaka S, Krueger AP (1978) Effects of Air Ions on microorganisms and Other Biological Materials. *Critical Reviews in Microbiology* **6(2)**, 109-150.

Kristjansson JE, Staple A, Kristiansen J, Kaas E (2002) A new look at possible connections between solar activity, clouds and climate. *Geophysical Research Letters* **29**.

Laut P (2003) Solar activity and terrestrial climate: an analysis of some purported correlations. *Journal of Atmospheric and Solar-Terrestrial Physics* **65**, 801-812.

Marsh N, Svensmark H (2000) Cosmic Rays, Clouds, and Climate. *Space Science Reviews* **94**, 215-230.

Mochan S, Gardiner B (2007) Timber Properties of Sitka Spruce from South Scotland: a study to identify causes of increased failure during stress grading. *Forest Research Internal Report.*

Morison JIL, Jarvis PG (1983) Direct and indirect effects of light on stomata. I. In Scots pine and Sitka spruce. *Plant, Cell and Environment* **6**, 95-101.

Morren G (1980) The rural ecology of the British drought of 1975–1976. *Human Ecology* **8**, 33-63.

Neilson RE, Jarvis PG (1975) Photosynthesis in Sitka Spruce (*Picea-Sitchensis (Bong.) Carr.*) .VI. Response of Stomata to Temperature. *Journal of Applied Ecology* **12**, 879-891.

Nevzgodina LV (1999) Chromosomal aberrations as a biomarker for cosmic radiation. *Fundamentals for the Assessment of Risks from Environmental Radiation* **55**, 203-208.

Pallé EP, Butler CJ (2000a) Sunshine, clouds and cosmic rays. *Proceedings of the 1st Solar and Space Weather EuroConference on the Solar Cycle and Terrestrial Climate* **463**, 147-152.

Pallé EP, Butler CJ (2000b) The influence of cosmic rays on terrestrial clouds and global warming. *Astronomy & Geophysics* **41**, 18-22.

Pallé E, Butler CJ, O'Brien K (2004) The possible connection between ionization in the atmosphere by cosmic rays and low level clouds. *Journal of Atmospheric and Solar-Terrestrial Physics* **66**, 1779-1790.

Phipps RL (1982) Comments on Interpretation of Climatic Information from Tree Rings Eastern North America. *Tree-Ring Bulletin* **42**, 11-22.

Pierce JR, Adams PJ (2009) Can cosmic rays affect cloud condensation nuclei by altering new particle formation rates? *Geophysical Research Letters* **36**.

Rigozo NR, Nordemann DJR, Echer E, da Silva HE, de Souza Echer MP, Prestes A (2007) Solar and climate imprint differences in tree ring width from Brazil and Chile. *Journal of Atmospheric and Solar-Terrestrial Physics* **69**, 449-458.

Rigozo NR, Nordemann DJR, Souza Echer MP, Echer E, da Silva HE, Prestes A, Guarnieri FL (2007) Solar activity imprints in tree ring width from Chile (1610-1991). *Journal of Atmospheric and Solar-Terrestrial Physics* **69**, 1049-1056.

Roderick ML (2006) The ever-flickering light. *Trends in Ecology & Evolution* **21**, 3-5.

Roderick M, Farquhar G, Berry S, Noble I (2001) On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. *Oecologia* **129**, 21-30.

Schimel DS (1995) Terrestrial ecosystems and the carbon cycle. *Global Change Biology* **1**, 77-91.

Schove DJ (1954) Summer Temperatures and Tree-Rings in North-Scandinavia A. D. 1461-1950. *Geografiska Annaler* **36**, 40-80.

Schweingruber FH (1988) Tree rings: basics and applications of dendrochronology. Kluwer Academic Publishers Dordrecht, Boston, 276 pp.

Siren G, Hari P (1971) Coinciding Periodicity in Recent Tree Rings and Glacial Clay Sediments. *Annales Universitatis Turkuensis Series A II Biologica-Geographica-Geologica* **47**, 155-157.

Spiecker H (1995) Growth dynamics in a changing environment — long-term observations. *Plant and Soil* **168-169**, 555-561.

Spiecker H (1999) Overview of Recent Growth Trends in European Forests. *Water, Air, & Soil Pollution* **116**, 33-46.

Stanhill G, Cohen S (2001) Global dimming: a review of the evidence for a widespread and significant reduction in global radiation with discussion of its probable causes and possible agricultural consequences. *Agricultural and Forest Meteorology* **107**, 255-278.

Sun BM, Bradley RS (2002) Solar influences on cosmic rays and cloud formation: A reassessment. *Journal of Geophysical Research-Atmospheres* **107**.

Suzaki T, Kume A, Ino Y (2003) Evaluation of direct and diffuse radiation densities under forest canopies and validation of the light diffusion effect. *Journal of Forest Research* **8**, 283-290.

Svensmark H, Friis-Christensen E (1997) Variation of cosmic ray flux and global cloud coverage - A missing link in solar-climate relationships. *Journal of Atmospheric and Solar-Terrestrial Physics* **59**, 1225-1232.

Svensmark H, Pedersen JOP, Marsh ND, Enghoff MB, Uggerhoj UI (2007) Experimental evidence for the role of ions in particle nucleation under atmospheric conditions. *Proceedings of the Royal Society - Mathematical Physical and Engineering Sciences* **463**, 385-396.

UK MetOffice (ed.) 2003. News release; 2003 Summary.
http://www.metoffice.gov.uk/climate/uk/interesting/2003summary.html (11.08.2009).

UK MetOffice (ed.) 2008a. News release.
http://www.metoffice.gov.uk/climate/uk/2008/march.html (11.08.2009).

UK MetOffice (ed.) 2008b. News release. UK climate. 2008 summary.
http://www.metoffice.gov.uk/climate/uk/2008/summer.html (11.08.2009).

Urban O, Janous D et al. (2007) Ecophysiological controls over the net ecosystem exchange of mountain spruce stand. Comparison of the response in direct vs. diffuse solar radiation. *Global Change Biology* **13**, 157-168.

Waring RH, Running, SW (1998) Forest ecosystems. Analysis at Multiple Scale. 370 pp.

Williams A, Still C, Fischer D, Leavitt S (2008) The influence of summertime fog and overcast clouds on the growth of a coastal Californian pine: a tree-ring study. *Oecologia* **156**, 601-611.

Yu FQ, Turco RP (2000) Ultrafine aerosol formation via ion-mediated nucleation. *Geophysical Research Letters* **27**, 883-886.

Zhang R (2007) Modelling carbon dioxide and water fluxes over European forests. *PhD Thesis*, The University of Edinburgh.

# Chapter 5

## General Discussion, Conclusions and Recommendations

# 5. General Discussion, Conclusions and Recommendations

The hypotheses linked to the current study are (i) that Sitka spruce [*Picea sitchensis (Bong.) Carr.*] is photosynthesising in a more efficient way under diffuse conditions than under clear skies, (ii) stomatal conductance is enhanced by diffuse radiation and (iii) the combined effects of diffuse radiation seen in the analysis of growth rings referring to long-term data on direct and diffuse radiation in Northern Britain. In order to test the above hypotheses a variety of measurements and analyses had to be carried out in Harwood, Griffin, and Forest of Ae, as well as by including meteorological data from Eskdalemuir (Observatory) in Southern Scotland. Here we revisit the hypotheses, one by one.

## 5.1. Attenuation of solar radiation by forest canopies

Helms (1965) was probably the first to observe an increase in carbon assimilation by coniferous trees under diffuse versus direct light. He studied Douglas Fir, [*Pseudotsuga menziesii*] in natural stands near Seattle, enclosing shoots from the middle of the canopy in chambers to make the gas exchange measurements. His work was largely ignored and even today is hardly cited. The general phenomenon has however now been widely established by Gu *et al.* (1999) and others who have been able to use the modern techniques of eddy covariance to study gas exchange of whole canopies. Several groups have seized upon this work, and speculated about its global significance, especially in relation to industrial aerosols (Farquhar & Roderick, 2003; Mercado *et al.*, 2009). Farquhar & Roderick (2003); Krakauer & Randerson (2003); Robock (2005) and Battipaglia *et al.* (2007) speculated on the increase in photosynthesis after the Pinatubo eruption in 1991, when the fraction of diffuse radiation increased globally.

This increase in carbon assimilation under diffuse conditions is also reflected in the current study (**paper II** and **paper III**). The mechanism behind this phenomenon is often related to the changes in sky conditions as being the driver for the enhanced carbon assimilation by plants.

Solar radiation measurements carried out above the forest canopy in Griffin Forest (**paper I**) have shown that the spectral distribution of incoming solar radiation is very similar under a variety of sky conditions, from clear skies to overcast conditions. Although these spectral properties were very similar, the amount of the photosynthetic active radiation (PAR) varied considerably. The assumption of diffuse radiation being more efficiently used by forests can, therefore, not be related to the spectral distribution of the incoming solar radiation. This result leads to the suggestion that it is not the spectral distribution above the forest canopy that leads to an increase in $CO_2$ uptake, but the radiation regime inside the canopy produced by the Sitka spruce forest stand itself under these diverse sky conditions.

Profound differences in the distribution of solar radiation occur, according to the different sky conditions. The most important of these seems to be the extent to which the direct sunlight is absorbed or reflected near the top of the canopy, shown by the attenuation patterns in **paper I**. The radiation is therefore not available for photosynthesis lower down in the canopy. Many have followed Monsi & Saeki (1953) in a 'classical' analysis of the light penetration into leaf canopies, which as a *first approximation* follows the Beer-Lambert extinction law. The present study shows, it to be a poor 'law' for coniferous canopies, not surprisingly because the Beer-Lambert law was devised for homogeneous conditions, such as a solution of coloured material in a spectrophotometer cell. Only computer intensive techniques like ray-tracing can deal with the complexity of real canopies of leaves, which are non-random. Certainly the Beer-Lambert law does not take into account the difference between direct and diffuse radiation (Balster & Marshall, 2000), nor does it describe the complexity of the radiation field to which the leaves are exposed, neither the spatial, nor the temporal distribution, because the forest canopy is not homogeneous (**paper I**).

The diffuse radiation inside a forest canopy includes the fraction scattered by the foliage itself as well as radiation transmitted through the leaves and through the many gaps (Muller, 1971; Lee, 1987; Grant, 1997).

It is not surprising that our investigations show that radiation penetration through the canopy under sunny conditions demonstrates only a poor fit to the Beer-Lambert Law (**paper I**), as was also shown by Norman & Jarvis (1974) and Lewandowska *et al.* (1977) in the same species, who obtained similar *k*-values to those reported in the current study. It is also shown, using an independent technique, the extent to which the diffuse radiation is relatively enhanced at the forest floor and by the distribution of ground-level data between transmission classes (**paper I**). This general feature was also shown by others (Morgan *et al.,* 1985; Leuchner *et al.,* 2005) and most notably by Navrátil *et al.* (2007) and Urban *et al.* (2007) who worked on a species of *Picea*.

Under clear skies gaps in the crown create highly illuminated areas where the incident light can *in extremis* reach higher values than above the canopy itself due to a high proportion of scattering of radiation on the surrounding branches (Muller, 1971; Kuppers *et al.,* 1997). These illuminated areas may create stress, such as photoinhibition (Powles, 1984; Krause, 1988; Long & Humphries, 1994) and water deficit (Kaufmann, 1976, 1979). Furthermore these gaps or sunflecks exhibit similar spectra (**paper I**; **Appendix II** - 0, 1 and 11 m above ground) to the incident radiation. The present study showed conclusively that the radiation regime (quantity and spectral distribution) inside the Sitka spruce [*Picea sitchensis (Bong.) Carr.*] forest is more evenly distributed under diffuse skies (cloudy, overcast) than under clear skies (**paper I**).

Others have studied light from a strictly physiological perspective. Smith (1982) indicated that a the blue-absorbing photoreceptor may act to measure light quantity (amount) and that the pigment phytochrome is possibly acting to detect the red:far-red ratio (R:FR) as an indicator of light quality, and a signal to which many photomorphologic processes respond, for example extension growth.

This R:FR ratio is attenuated drastically inside the forest canopy (**paper I**) under clear skies indicating a different photomorphological behaviour than under diffuse skies. Ritchie (1997) went one stage further, noting that trees have the ability to detect nearby trees and may adjust their growth allometry accordingly. Low R:FR has long been known to increase stem elongation (Smith, 1982; Corre, 1983; Ballare *et al.*, 1991; Assmann, 1992; de la Rosa *et al.*, 1998; Franklin & Whitelam, 2005; Pecot *et al.*, 2005).

Another aspect of light quality which is playing a mayor role in plant plantations, (**paper I** and **paper II**), is row spacing. Managed forest plantations in which row thinning has occurred are affected by a lateral shift in the amount and quality of solar radiation reaching the forest floor under various sky conditions. This ecophysiological aspect has been described in detail in the current study (**paper I**) and results presented, showing a reduced R:FR ratio in the canopy under clear skies, indicating a lower photomorphogenical 'light quality' (*sensu* Smith, 1982) than under diffuse conditions.

Along with an enhanced PAR distribution inside the forest canopy due to reflection, scattering and transmission under cloudy and overcast conditions, we noted an obvious blue light enrichment throughout the canopy (**paper I**). Blue-enrichment may have important implications for stomatal control, and new studies on stomatal response under canopies are now required (see **Recommendations**).

We proposed the hypothesis that Sitka spruce is photosynthesising in a more efficient way under diffuse sky conditions than under clear skies (**paper I**, **paper II** and **paper III**). This hypothesis is supported by the fit of the rectangular hyperbola (Watts *et al.*, 1976; Jarvis, 1987; Causton & Dale, 1990; Jarvis, 1994; Raupach, 1995; Ruimy *et al.*, 1995) to the data under different sky conditions (**paper II**). In all cases the fitted values of the maximum gross photosynthesis ($A_{max}$) are less when conditions are sunny. In most cases the initial slope of the light response curve is lower in the sunny conditions indicating a reduced apparent quantum efficiency of the canopy (**paper II**). Other researchers have found similar results in Aspen (Gu *et* *al.,* 1999), in Norway spruce (Urban *et al.,* 2007), a mixed hardwood and conifer forest (Min, 2005), various ecosystems (Law *et al.,* 2002; Alton *et al.,* 2007) in light response models (Zhang, 2007; Still et al., 2009), and was found in one species of woody shrub (Grace & Woolhouse, 1973). Further studies on non-forest species are required.

## 5.2. Effect of diffuse radiation on stomatal conductance in the canopy

We now address the second hypothesis.
Solar radiation plays a lead role in driving photosynthesis of plants but is modified by canopy conductance, which responds to both environmental and physiological variables to protect the plant from worse effects of water stress (Kaufmann, 1976; Zeiger, 1983, 1990). It has been shown that diffuse light penetrates more deeply into the Sitka spruce canopy (**paper I**), and may also have spectral characteristics that elicit stomatal opening (**paper I** and **paper II**). Penetration of light into the forest canopy under diffuse conditions, due to transmission of light through needles and possibly as a result of multiple reflections and scattering involving the waxy abaxial surfaces of coniferous needles (Jeffree *et al.,* 1971; Reicosky & Hanover, 1978; Cape & Percy, 1993) are creating a light regime which stomata may respond to, and open more widely. In the present study we were not able to distinguish between a response of stomata to blue light, and the well-known response to VPD, as diffuse conditions are frequently associated with low VPDs. Thus cloudy, foggy, overcast skies are frequently associated with moist air. We propose a dual control mechanism (Fig. 5.1a) acknowledging both possible controls.

The second hypothesis linked to the current study is that the photosynthetic response of *Picea sitchensis* is constrained by stomatal conductance which varies between conditions of direct versus diffuse radiation (**paper II**).

In **paper II** we have already reviewed the relevant literature on the blue light effect. It is noteworthy that the action spectrum is now well-established (Kuiper, 1964; Karlsson, 1986) with a peak around 450 nm.

In the same species as currently used Morison & Jarvis (1983) show that $g_c$ is very sensitive to blue light which elicited stomatal opening in a range of 0 - 300 μmol $m^{-2}$ $s^{-1}$. In the current study (**paper II**) we find that it is within the same range, that the observed values of $g_c$ are often much-elevated in diffuse conditions, allowing higher rates of photosynthesis. We also know (**paper I**) that under diffuse conditions, Sitka spruce forests experience an enriched blue light regime inside and below the canopy, and so producing their own, possibly optimal, light regime surrounding the photosynthesising foliage.

Measurements carried out in the closely related Norway spruce (*Picea abies*) (Urban *et al.*, 2007) show similar results to those estimated for Sitka spruce (**paper II**). However, Urban et al. (2007) found, that sunny conditions with PAR values higher than 600 μmol $m^{-2}$ $s^{-1}$ impaired $g_c$, a feature they attributed to high VPD which often accompanies sunny weather. VPD values in the current study rarely exceeded 2 kPa. Early measurements show that *Picea sitchensis* is very sensitive to VPD, with a $g_c$ response that is approximately linear (Grace *et al.*, 1975; Neilson & Jarvis, 1975). In Sitka spruce forests, where long term heat stress is rare due to the oceanic climate they grow in, diffuse radiation and VPD become of very high importance.

### 5.3. Long-term trends in diffuse radiation and implications for tree ring research

The third hypothesis addresses possible long term effects. As pointed out above, many authors have speculated about long term trends, and tried to model them. However, there are now long term observations of forest response to diffuse radiation. Measurements carried out in Harwood and Griffin forest over the 2008 growing season included in the current study represent only one growing season (**paper II**). Data from only one growing season may not be representative, and may not be a reliable guide to forest growth over longer periods. Therefore a long-term study was designed, serving to investigate the possible link of climatological variables, such as diffuse radiation and forest growth, over several decades (**paper III**).

As previously observed, there is a link between canopy photosynthesis and canopy conductance partly in conjunction with VPD influence (**paper II**). Results from tree ring analysis indicate correlations between the annual growth anomaly and VPD (**paper III**). VPD has long been known to influence photosynthesis for the reason that the stomata close when the air is dry, especially in this species (Grace *et al.*, 1975; Neilson & Jarvis, 1975). Cloudiness, *per se* may be expected to reduce plant growth through a reduction in solar insolation, although Williams *et al.* (2008) have found that the effect of cloud cover on tree growth, and thus ring width, may vary depending on the type of cloud, the time of day, and the time of year.

We were surprised to see that the cosmic ray flux was always statistically significantly correlated with the growth index, with correlation coefficients that exceed all others in the analysis. The first presumption was that cosmic rays create aerosols and thus change the radiation field.

In cloud physics the subject is highly controversial. Svensmark & Friis-Christensen (1997); Marsh & Svensmark (2000); Pallé & Butler (2000a, 2000b) show relationships between cloud cover and the galactic cosmic ray (GCR) flux. These observations have been challenged (Kristjansson *et al.*, 2002; Sun & Bradley, 2002; Laut, 2003). However, recent models (Kerr, 2009; Pierce & Adams, 2009) show only small effects of cosmic rays on clouds but are not denying the possibility of a link. Probably this issue will continue to be researched and debated by atmospheric scientists for many years.

To explain the link between GCRs, diffuse radiation and the growth anomaly we propose the possible hypothesis that the forest 'sees' a radiation field that is modified by the aerosol particles derived from the flux of cosmic rays, but not recordable with common solar radiation sensors. The study, introduced here (**paper III**), carried out in southern Scotland indicates a positive relationship between the growth of Sitka spruce trees and the amount of diffuse radiation available to the forest over the spring and summer months. Previous measurements in Sitka spruce (**paper II**) and in various other *Picea* species (Gu et al., 1999 and Urban et al., 2007) have related enhanced carbon dioxide uptake to diffuse radiation.

Cyclic phenomena in growth ring sequences have been reported (Douglass, 1927; Siren & Hari, 1971; Currie, 1991; Briffa, 1994; Rigozo *et al.*, 2007a, 2007b) but have not become part of the main agenda in tree ring research, perhaps because they are controversial and variable. We cannot however rule out the possibility of a direct stimulatory effect of GCR on the growth of trees, as beneficial effects have sometimes been demonstrated in biological materials exposed to GCR in space (Hammond *et al.,* 1996), despite the prevalence of chromosomal aberrations in such materials (Nevzgodina, 1999).

However, processes other than cosmic ray flux such as volcanic eruptions affect the flux of diffuse radiation received at the Earth's surface (Farquhar & Roderick, 2003; Krakauer & Randerson, 2003; Robock, 2005 and Battipaglia *et al.*, 2007) even when they are many thousands of miles away. In Fig. 5.1b we incorporate a role of cosmic rays and volcanism in the process of forest growth (**paper III**). These non-climatological processes have been neglected in the past, but may eventually be recognised as factors in determining long term forest growth and carbon storage.

No studies have been found to explain the pattern of diffuse radiation occurring in particular years, apart from general assumptions that the observed decrease in solar radiation is caused by the known phenomenon of global dimming (Roderick *et al.*, 2001; Stanhill & Cohen, 2001; Roderick, 2006). Furthermore, no direct links between global dimming and enhanced carbon dioxide uptake by plants were reported, since this phenomenon occurred simultaneous with an obvious increase in carbon dioxide in the atmosphere (Jacoby & D'Arrigo, 1997).

This study, however, shows a distinctive relationship between volcanic eruptions which occurred west to the United Kingdom and the pattern of diffuse radiation, recorded as the fraction of global radiation in Upland Scotland (**paper III**) over the past decades.

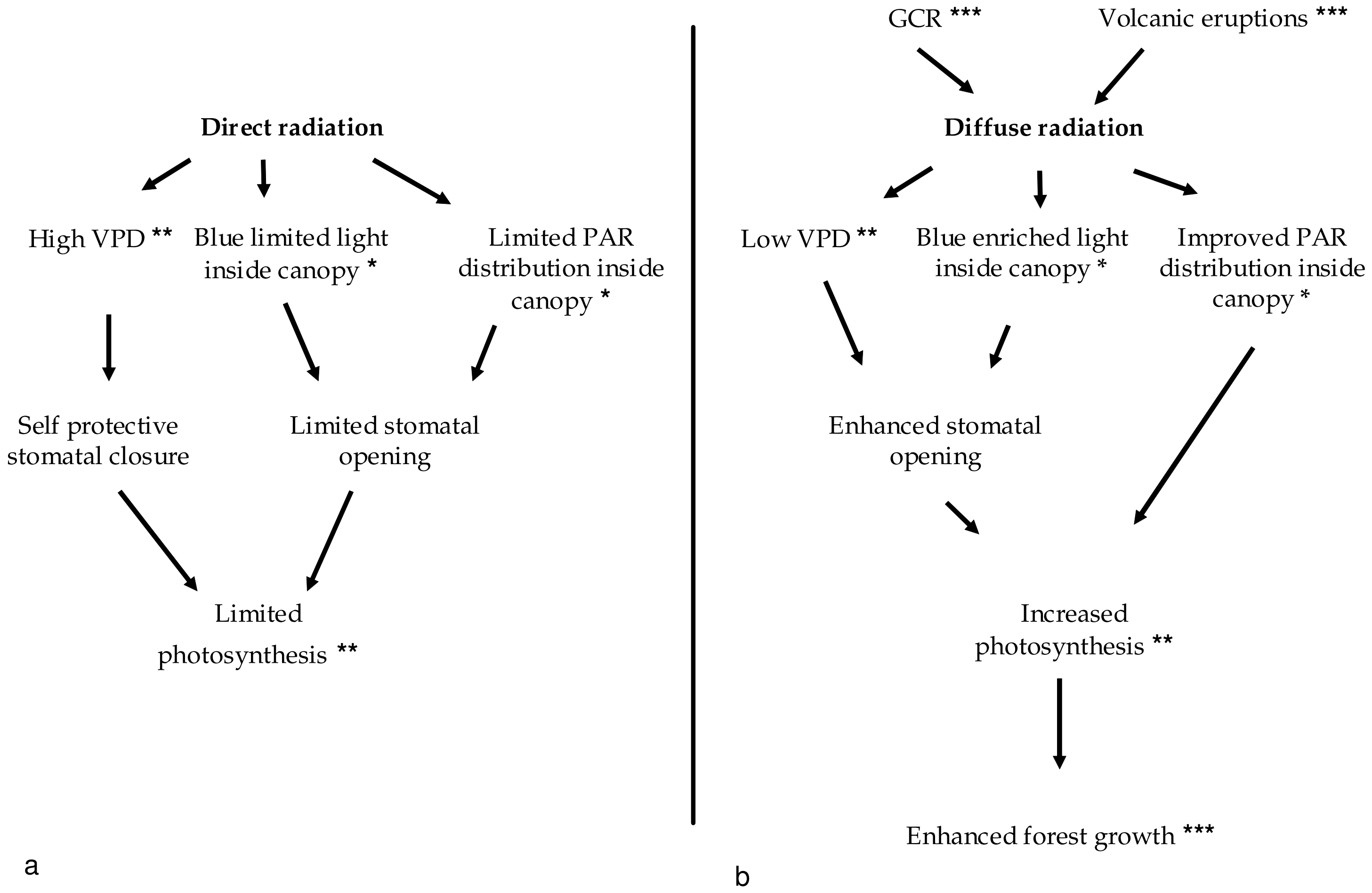


Figure 5.1: * Represents findings presented in paper I; ** represents findings from paper II and *** represent findings from paper III

## 5.4. Conclusions and recommendations

The main objectives of the present study were the investigation of sky conditions and their influence on the carbon dioxide uptake by forests in Northern Britain. We have shown long-term data on direct and diffuse solar radiation from Southern Scotland and how its distribution and pattern has been directly (volcanic eruptions) and hypothetically (galactic cosmic rays) influenced over the past decades. We know that forests are assimilating carbon in a much more efficient way under diffuse conditions and are also leading to increased forest growth. By studying how different cloud conditions can affect carbon uptake we can understand how forests might respond to changes in cloud cover. Such mechanisms and linkages are important to quantify and predict the impact of climate change on rates of forest growth in the future.

We have shown that solar radiation (including photosynthetic active radiation) is penetrating deeper into the Sitka spruce [*Picea sitchensis (Bong.) Carr.*] forest canopy under various diffuse skies compared to clear skies. We have shown that diffuse radiation is distributed more evenly inside the forest and with it there is more blue light surrounding the photosynthesising foliage. There is evidence from previous studies that this diffuse radiation is especially conducive to stomatal opening because it is blue-enriched. In the long-term this is translated into enhanced forest growth (carbon accumulation) of *Picea sitchensis* under diffuse conditions in Southern Upland Scotland.

The canopy does not achieve its highest photosynthetic rates, nor its highest stomatal conductance when solar radiation is dominated by direct solar radiation. In overcast conditions, when solar radiation is 100% diffuse, blue light enrichment and low vapour pressure deficit may both contribute to an enhanced photosynthetic performance.

The main conclusions are best represented as an influence diagram (Fig. 5.1a & b).

The research introduced here should not be seen as the final word; several recommendations are suggested in order to refine and also to support the current results.

- We recommend a more intense campaign of spectral measurements in Griffin forest (**paper I**) over a wide range of sky conditions, and during all hours of the day, in order to receive diurnal estimates of radiation penetration and spectral distribution of light.
- Repeating the spectral measurements (**paper I**), mentioned above, by adding reflectance and fluorescence measurements (the radiometer just needs to be pointed downwards, as opposed to upwards as used in the study presented here).
- Further clarification of whether blue light or reduced VPD causes the effect of enhanced stomatal activity (**paper II**) cannot be made without experimental studies inside the canopy. VPD would need to be held constant in chambers, whilst blue light would have to be manipulated.
- An investigation of long-term (several growing seasons) direct versus diffuse solar radiation and eddy covariance data in order to investigate the light responses over the different growing periods and also integrate a canopy conductance - diffuse radiation study for Sitka spruce in Northern Britain (**paper II**). This study could be done with existing eddy covariance data sets although most sites and most researchers have not installed either the sunshine sensor or classical shade-ring solarimeters.
- Galactic cosmic rays (**paper III**) are latitude dependent. Since no further studies were found looking at the relationship between tree ring width and galactic cosmic rays, we suggest an investigation into tree ring data from other northern latitude and cosmic rays in order to support the current results.

## 5.5. References

Alton PB, North PR, Los SO (2007) The impact of diffuse sunlight on canopy light-use efficiency, gross photosynthetic product and net ecosystem exchange in three forest biomes. *Global Change Biology* **13**, 776-787.

Assmann SM (1992) Effects of light quantity and quality during development on the morphology and stomatal physiology of Commelina communis. *Oecologia* **92**, 188-195.

Ballaré CL, Scopel AL, Sánchez RA (1991) Photocontrol of stem elongation in plant neighbourhoods: effects of photon fluence rate under natural conditions of radiation. *Plant, Cell and Environment* **14**, 57-65.

Balster NJ, Marshall JD (2000) Eight-year responses of light interception, effective leaf area index, and stemwood production in fertilized stands of interior Douglas-fir (*Pseudotsuga menziesii var. glauca*). *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **30**, 733-743.

Battipaglia G, Cherubini P, Saurer M, Siewolf RT, Strumia S, Cotrufo F (2007) Volcanic explosive eruptions of the Vesuvio decrease tree-ring growth but not photosynthetic rates in the surrounding forests. *Global Change Biology* **13**,1122-1137.

Briffa KR (1994) Grasping at shadows? A selective review of the search for sunspot-related variability in tree rings. *The Solar Engine and Its Influence on Terrestrial Atmosphere and Climate* **I 25**, 417–434.

Cape JN, Percy KE (1993) Environmental Influences on the Development of Spruce Needle Cuticles. *New Phytologist* **125(4)**, 787-799.

Causton DR, Dale MP (1990) The Monomolecular and Rectangular Hyperbola as Empirical-Models of the Response of Photosynthetic Rate to Photon Flux-Density, with Applications to 3 Veronica Species. *Annals of Botany* **65**, 389-394.

Corre W (1983) Growth and morphogenesis of sun and shade plants. II. The influence of light quality. *Acta Botanica Neerlandica* **32**, 185-202.

Currie RG (1991) Deterministic Signals in Tree-Rings from North-America. *International Journal of Climatology* **11**, 861-876.

de la Rosa TM, Aphalo PJ, Lehto T (1998) Effects of far-red light on the growth, mycorrhizas and mineral nutrition of Scots pine seedlings. *Plant and Soil* **201**, 17-25.

Douglass AE (1927) Solar Records in Tree Growth. *Science* **65**, 220-221.

Farquhar GD, Roderick ML (2003) Atmospheric science: Pinatubo, diffuse light, and the carbon cycle. *Science* **299**, 1997-1998.

Franklin KA, Whitelam GC (2005) Phytochromes and Shade-avoidance Responses in Plants. *Annals of Botany* **96**, 169-175.

Grace J, Malcolm DC, Bradbury IK (1975) The Effect of Wind and Humidity on Leaf Diffusive Resistance in Sitka Spruce Seedlings. *The Journal of Applied Ecology* **12**, 931-940.

Grace J, Woolhouse HW (1973) A Physiological and Mathematical Study of the Growth and Productivity of a *Calluna-sphagnum* Community. II. Light Interception and Photosynthesis in Calluna. *Journal of Applied Ecology* **10**, 63-76.

Grant R (1997) Partitioning of biologically active radiation in plant canopies. *International Journal of Biometeorology* **40**, 26-40.

Gu L, Fuentes JD, Shugart HH, Staebler RM, Black TA (1999) Responses of net ecosystem exchanges of carbon dioxide to changes in cloudiness: Results from two North American deciduous forests. *Journal of Geophysical Research* **104**.

Hammond EC, Bridgers K, Berry FD (1996) Germination, growth rates, and electron microscope analysis of tomato seeds flown on the LDEF. *Radiation Measurements* **26**, 851-861.

Helms JA (1965) Diurnal and Seasonal Patterns of Net Assimilation in Douglas-Fir, *Pseudotsuga Menziesii (Mirb). Franco*, as Influenced by Environment. *Ecology* **46**, 698-708.

Jacoby GC, D'Arrigo R (1997) Tree rings, carbon dioxide, and climatic change. *Proceedings of the National Academy of Sciences* **94**, 8350-8353.

Jarvis PG (1987) Water and Carbon Fluxes in Ecosystems. Schulze, E.-D. and H. Zwoelfer (Ed.). *Ecological Studies Analysis and Synthesis* **61**. Potentials and Limitations of Ecosystem Analysis. 50-67.

Jarvis PG (1994) Capture of Carbon Dioxide by a Coniferous Forest. *Resource Capture by Crops*, 351-374.

Jeffree CE, Johnson RPC, Jarvis PG (1971) Epicuticular wax in the stomatal antechamber of sitka spruce and its effects on the diffusion of water vapour and carbon dioxide. *Planta* **98**, 1-10.

Karlsson PE (1986) Blue light regulation of stomata in wheat seedlings. II. Action spectrum and search for action dichroism. *Physiologia Plantarum* **66**, 207-210.

Kaufmann MR (1976) Stomatal Response of Engelmann Spruce to Humidity, Light, and Water Stress. *Plant Physiology* **57**, 898-901.

Kaufmann MR (1979) Stomatal control and the development of water deficit in Engelmann spruce seedlings during drought. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **9**, 297-304.

Kerr RA (2009) Study Challenges Cosmic Ray-Climate Link. *Science* **324**, 576-577.

Krakauer NY, Randerson JT (2003) Do volcanic eruptions enhance or diminish net primary production? Evidence from tree rings. *Global Biogeochemical Cycles* **17(4)**, 11 pp.

Krause GH (1988) Photoinhibition of photosynthesis. An evaluation of damaging and protective mechanisms. *Physiologia Plantarum* **74**, 566-574.

Kristjansson JE, Staple A, Kristiansen J, Kaas E (2002) A new look at possible connections between solar activity, clouds and climate. *Geophysical Research Letters* **29**.

Kuiper PJC (1964) Dependence upon Wavelength of Stomatal Movement in Epidermal Tissue of Senecio odoris. *Plant Physiology* **39**, 952-955.

Kuppers M, Timm H, Orth F, Stegemann J, Stober R, Schneider H, Paliwal K, Karunaichamy KSTK, Ortiz R (1996) Effects of light environment and successional status on lightfleck use by understory trees of temperate and tropical forests. *Tree Physiology* **16**, 69-80.

Laut P (2003) Solar activity and terrestrial climate: an analysis of some purported correlations. *Journal of Atmospheric and Solar-Terrestrial Physics* **65**, 801-812.

Law BE, Falge E, et al. (2002) Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agricultural and Forest Meteorology* **113**, 97-120.

Lee DW (1987) The Spectral Distribution of Radiation in Two Neotropical Rainforests. *Biotropica* **19**, 161-166.

Leuchner M, P. Fabian H. Werner (2005) Spectral Multichannel Monitoring of Radiation within a Mature Mixed Forest. *Plant Biology* **7**, 619-627.

Lewandowska M, Hart JW, Jarvis PG (1977) Photosynthetic Electron Transport in Shoots of Sitka Spruce from Different Levels in a Forest Canopy. *Physiologia Plantarum* **41**, 124-128.

Long SP, Humphries S, Falkowski PG (1994) Photoinhibition of Photosynthesis in Nature. *Annual Review of Plant Physiology and Plant Molecular Biology* **45**, 633-662.

Marsh N, Svensmark H (2000) Cosmic Rays, Clouds, and Climate. *Space Science Reviews* **94**, 215-230.

Mercado LM, Bellouin N, Sitch S, Boucher O, Huntingford C, Wild M, Cox PM (2009) Impact of changes in diffuse radiation on the global land carbon sink. *Nature* **458**, 1014-1017.

Min Q (2005) Impacts of aerosols and clouds on forest-atmosphere carbon exchange. *Journal of Geophysical Research* **110**.

Monsi M, Saeki T (2005) On the Factor Light in Plant Communities and its Importance for Matter Production. *Annals of Botany* **95**, 549-567. Orig. 1953, Über den Lichtfactor in der Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion, *Japanese Journal of Botany* **14**, 22-52.

Morgan DC, Warrington IJ, Rook DA (1985) Some observations on the spectral distribution characteristics of short-wave radiation within *Pinus radiate D. Don* canopies. *Plant, Cell and Environment* **8**, 201-206.

Morison JIL & Jarvis PG (1983) Direct and indirect effects of light on stomata. I. In Scots pine and Sitka spruce. *Plant, Cell and Environment* **6**, 95-101.

Muller RA (1971) Transmission components of solar radiation in pine stands in relation to climatic and stand variables. *Pacific Southwest Forest & Range Experiment Station, Forest Service, U.S. Department of Agriculture*; 13 pp.

Navrátil M, Špunda V, Marková I, Janouš D (2007) Spectral composition of photosynthetically active radiation penetrating into a Norway spruce canopy: the opposite dynamics of the blue/red spectral ratio during clear and overcast days. *Trees - Structure and Function* **21**, 311-320.

Neilson RE, Jarvis PG (1975) Photosynthesis in Sitka Spruce (*Picea-Sitchensis (Bong) Carr.*) .VI. Response of Stomata to Temperature. *Journal of Applied Ecology* **12**, 879-891.

Nevzgodina LV (1999) Chromosomal aberrations as a biomarker for cosmic radiation. *Fundamentals for the Assessment of Risks from Environmental Radiation* **55**, 203-208.

Norman JM, Jarvis PG (1974) Photosynthesis in Sitka Spruce (*Picea sitchensis (Bong.) Carr.*). III. Measurements of Canopy Structure and Interception of Radiation. *Journal of Applied Ecology* **11**, 375-398.

Pallé E, Butler CJ (2000a) Sunshine, clouds and cosmic rays. *Proceedings of the 1st Solar and Space Weather Euroconference on the Solar Cycle and Terrestrial Climate* **463**, 147-152.

Pallé E, Butler CJ (2000b) The Influence of cosmic rays on terrestrial clouds and global warming. *Astronomy & Geophysics* **41**, 18-22.

Pecot SD, Horsley SB, Battaglia MA, Mitchell RJ (2005) The influence of canopy, sky condition, and solar angle on light quality in a longleaf pine woodland. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **35**, 1356-1366.

Pierce JR, Adams PJ (2009) Can cosmic rays affect cloud condensation nuclei by altering new particle formation rates? *Geophysical Research Letters* **36**.

Powles SB (1984) Photoinhibition of Photosynthesis Induced by Visible Light. *Annual Review of Plant Physiology* **35**, 15-44.

Raupach MR (1995) Vegetation Atmosphere Interaction and Surface Conductance at Leaf, Canopy and Regional Scales. *Agricultural and Forest Meteorology* **73**, 151-179.

Reicosky DA, Hanover JW (1978) Physiological Effects of Surface Waxes: I. Light Reflectance for Glaucous and Nonglaucous Picea pungens. *Plant Physiology* **62**, 101-104.

Rigozo NR, Nordemann DJR, Echer E, da Silva HE, de Souza Echer MP, Prestes A (2007) Solar and climate imprint differences in tree ring width from Brazil and Chile. *Journal of Atmospheric and Solar-Terrestrial Physics* **69**, 449-458.

Rigozo NR, Nordemann DJR, Souza Echer MP, Echer E, da Silva HE, Prestes A, Guarnieri FL (2007) Solar activity imprints in tree ring width from Chile (1610-1991). *Journal of Atmospheric and Solar-Terrestrial Physics* **69**, 1049-1056.

Ritchie GA (1997) Evidence for red:far red signaling and photomorphogenic growth response in Douglas-fir (*Pseudotsuga menziesii*) seedlings. *Tree Physiology* **17**, 161-168.

Robock A (2005) Cooling following large volcanic eruptions corrected for the effect of diffuse radiation on trees. *Geophysical Research Letters* **32**, 4 pp.

Roderick ML (2006) The ever-flickering light. *Trends in Ecology & Evolution* **21**, 3-5.

Roderick M, Farquhar G, Berry S, Noble I (2001) On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. *Oecologia* **129**, 21-30.

Ruimy A, Jarvis PG, Baldocchi DD, Saugier B (1995) $CO_2$ Fluxes over Plant Canopies and Solar Radiation: A Review. *Advances in Ecological Research* **26**.

Siren G, Hari P (1971) Coinciding Periodicity in Recent Tree Rings and Glacial Clay Sediments. *Annales Universitatis Turkuensis Series A II Biologica-Geographica-Geologica* **47**, 155-157.

Smith H (1982) Light Quality, Photoperception, and Plant Strategy. *Annual Review of Plant Physiology* **33**, 481-518.

Stanhill G, Cohen S (2001) Global dimming: a review of the evidence for a widespread and significant reduction in global radiation with discussion of its probable causes and possible agricultural consequences. *Agricultural and Forest Meteorology* **107**, 255-278.

Still CJ, Riley WJ, et al. (2009) Influence of clouds and diffuse radiation on ecosystem-atmosphere $CO_2$ and $CO^{18}O$ exchanges. *Journal of Geophysical Research* **114**.

Sun BM, Bradley RS (2002) Solar influences on cosmic rays and cloud formation: A reassessment. *Journal of Geophysical Research-Atmospheres* **107**.

Svensmark H, Friis-Christensen E (1997) Variation of cosmic ray flux and global cloud coverage - A missing link in solar-climate relationships. *Journal of Atmospheric and Solar-Terrestrial Physics* **59**, 1225-1232.

Svensmark H, Pedersen JOP, Marsh ND, Enghoff MB, Uggerhoj UI (2007) Experimental evidence for the role of ions in particle nucleation under atmospheric conditions. *Proceedings of the Royal Society; a - Mathematical Physical and Engineering Sciences* **463**, 385-396.

Urban O, Janous D, et al. (2007) Ecophysiological controls over the net ecosystem exchange of mountain spruce stand. Comparison of the response in direct vs. diffuse solar radiation. *Global Change Biology* **13**, 157-168.

Watts WR, Neilson RE, Jarvis PG (1976) Photosynthesis in Sitka Spruce (*Picea sitchensis (Bong,) Carr.*): VII. Measurements of Stomatal Conductance and $^{14}CO_2$ Uptake in a Forest Canopy. *Journal of Applied Ecology* **13**, 623-638.

Williams A, Still C, Fischer D, Leavitt S (2008) The influence of summertime fog and overcast clouds on the growth of a coastal Californian pine: a tree-ring study. *Oecologia* **156**, 601-611.

Zeiger E (1983) The Biology of Stomatal Guard-Cells. *Annual Review of Plant Physiology and Plant Molecular Biology* **34**, 441-475.

Zeiger E (1990) Light perception in guard cells. *Plant, Cell and Environment* **13**, 739-744.

Zhang R (2007) Modelling carbon dioxide and water fluxes over European forests. *PhD thesis*, The University of Edinburgh.

# Chapter 6

## Appendix

# 6. Appendix

## 6.1. Appendix I

### 6.1.1. Setback - February 2006

Due to incorrect felling activity in Harwood Forest (Northumberland) early 2006 by Forest Enterprise and Forestry contractors and the elimination of a crucial part of the forest, the entire project experienced a setback of several months. The original Harwood forest research site which is served with mains power accommodated a 27 metre tall tripole mast which included the main eddy covariance and meteorological station mounted at the top. The site accommodated furthermore a shed, which housed the entire logging system. Access to the majority of the instrumentation was limited to certified climbers only. Due to this unfortunate incident the entire research site needed to be relocated.

The relocation meant finding another forest site, suitable for eddy covariance measurements. This technique ideally requires flat terrain and homogeneous same aged forest of at least 1km$^2$. Relocating the research site also required the relocation of mains power and installation of power cables along the forest floor, embedded in a trench or as overhead cables. Further delays were caused by the requirement of Planning Permission issued by Alnwick District Council in Northumberland (England).

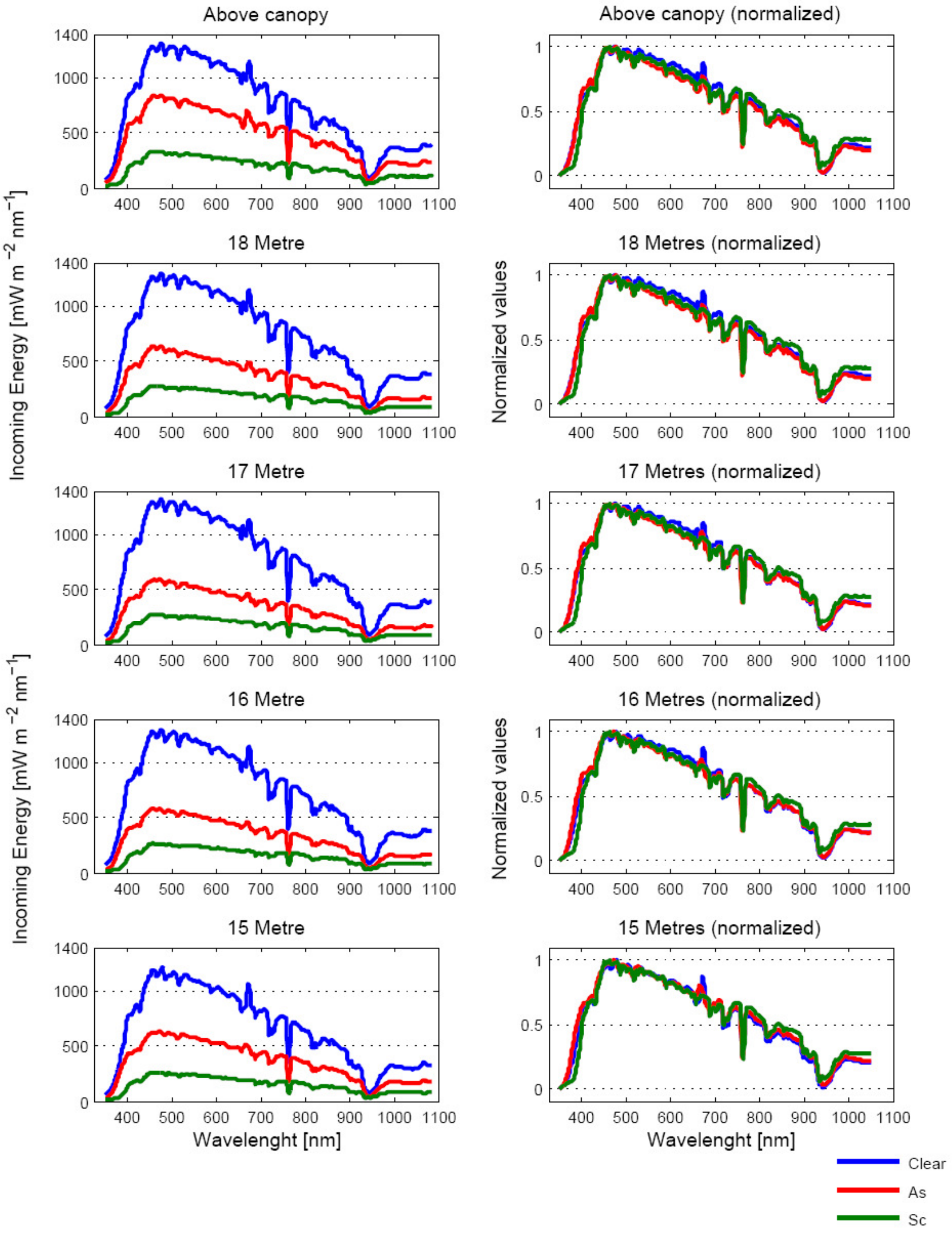
### 6.1.2. Recovery Plan and new sites

Due to the difficult accessibility of the original structure (tripole mast) it had been decided to upgrade to a walk-up tower in order to continue the project. The decision was to stay in Harwood Forest and to move into a younger plot. The original

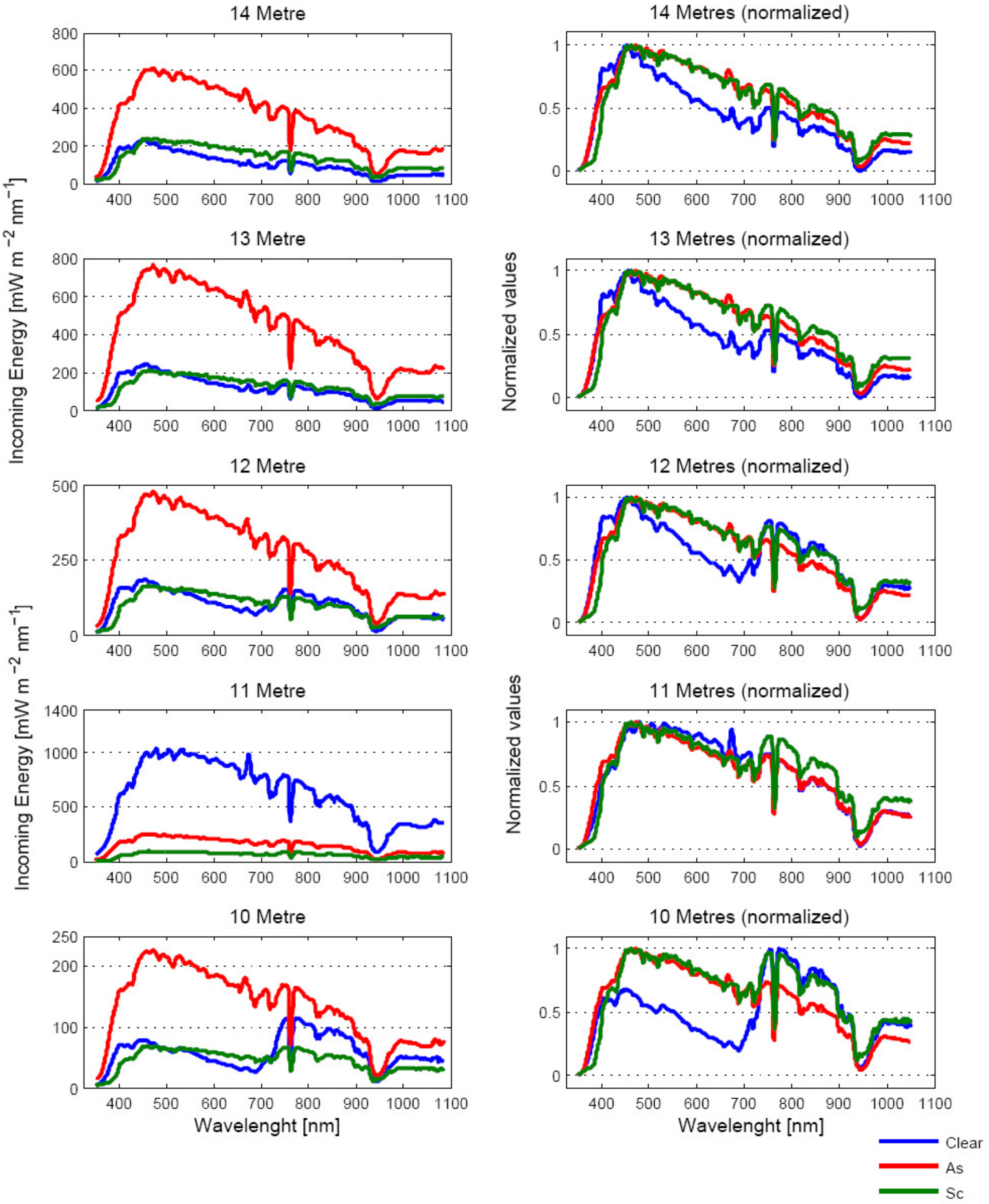
Harwood site was located in a 38 year old plot. The location of the new site was chosen to be in a 33 years (in 2009) old stand, north of the original site. The new site uses a walk-up tower, approximately 28m high. This construction design is a scaffolding tower and does not limit access or the number of sensors installed on top due to weight over load, which was faced at the original site. Planning permission was issued in December 2006, mains power cables were laid out in August 2007 with a functioning and running site in April 2008.

Three more sites have been integrated into the research project in order to fulfil all objectives and answer the set questions: Griffin Forest, Forest of Ae and Eskdalemuir Observatory (data only). Forest of Ae and Eskdalemuir were chosen in addition in order to combine short term with long term studies to investigate past changes in forest growth. Working in Griffin allowed us to do studies in a well managed forest plantation which had been row and selectively thinned in 2004.

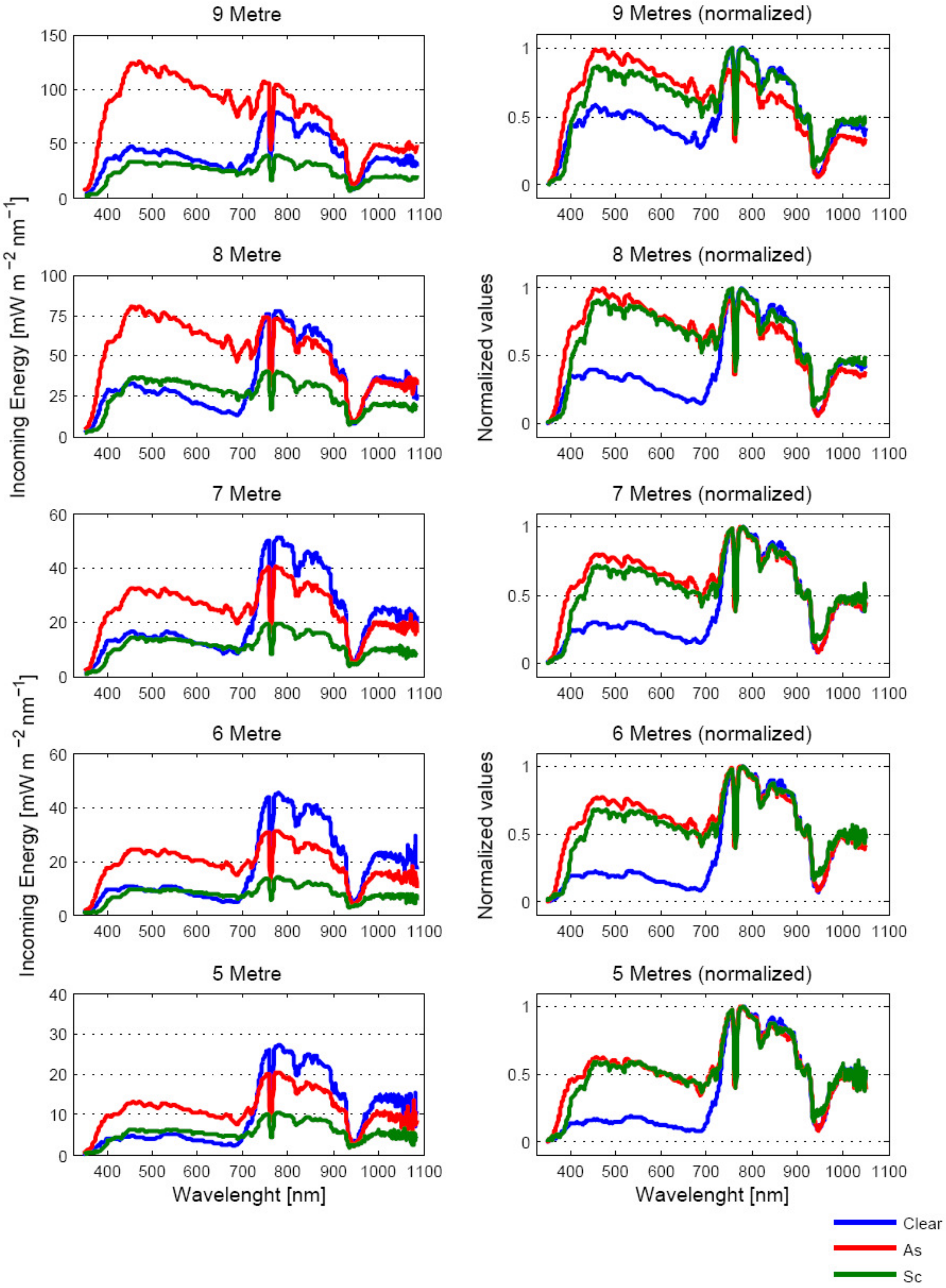
## 6.2. Appendix II



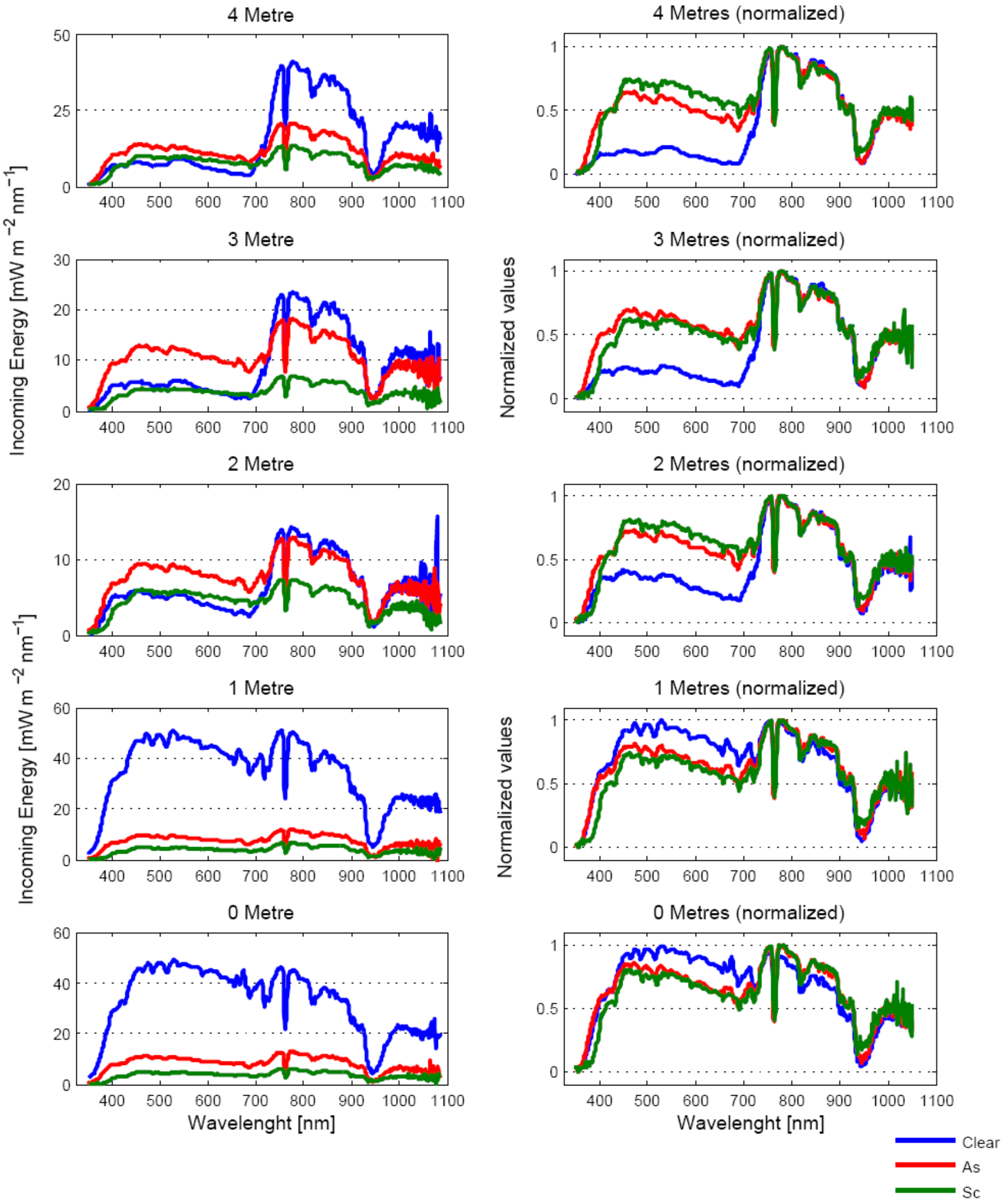
Mean spectra recorded along the Griffin eddy flux tower as one proceeds through the canopy. Part 1: 22 - 15 meters.



Mean spectra recorded along the Griffin eddy flux tower as one proceeds through the canopy.
Part 2: 14 - 10 meters.



Mean spectra recorded along the Griffin eddy flux tower as one proceeds through the canopy. Part 3: 9 - 5 meters.



Mean spectra recorded along the Griffin eddy flux tower as one proceeds through the canopy. Part 4: 4 - 0 meters.